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DE

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Description of five new species of *Holoparasitus* s. str. with redescription of *H. apenninorum* (Berlese, 1906) and *H. cultriger* (Berlese, 1906) from Italy and Spain (Acari, Gamasida, Parasitidae)

Ilinca JUVARA-BALS[1] & Wojciech WITALIÑSKI[2]
[1] Museum of Natural History, CP 6434, CH-1211 Geneva 6, Switzerland.
[2] Institute of Zoology, Jagiellonian University, Ingardena 6, PL-30060 Kraków, Poland.

Description of five new species of *Holoparasitus* s. str. with redescription of *H. apenninorum* (Berlese, 1906) and *H. cultriger* (Berlese, 1906) from Italy and Spain (Acari, Gamasida, Parasitidae). - The specimens included under the name of *H. apenninorum* (Berlese, 1906) in the Berlese collection in Florence are reviewed and a lectotype for *H. apenninorum* is designated. Five new species, *H. cornutus* sp. n., *H. crassisetosus* sp. n., *H. digitiformis* sp. n., *H. ellipticus* sp. n., *H. gibber* sp. n. are described and *H. cultriger* (Berlese, 1906) is redescribed, all from material from Italy and Spain. The characteristics of a new species group *mallorcae* is given.

Key-words: Acari - Gamasida - Parasitidae - *Holoparasitus* - taxonomy.

INTRODUCTION

The gamasids belonging to the genus *Holoparasitus* Oudemans, 1936 are free living, ground inhabiting predatory mites, distributed in the Holarctic region. This genus comprises 34 species which are divided, accordingly to Juvara-Bals (1975) and Hyatt (1987), into three subgenera: *Holoparasitus* s. str. (30 species), *Heteroparasitus* Juvara-Bals, 1975 (3 species) and *Ologamasiphis* Holzmann, 1969 (1 species).

In the subgenus *Holoparasitus* s. str., Micherdziñski (1969) distinguished two species-groups: *calcaratus* and *pollicipatus*-groups, whereas the remaining species are considered as *incertae sedis*. Juvara-Bals (1975) proposed another group of species, named *caesus*-group. More recently Hyatt (1987) mentioned only the species-groups recognized by Micherdzinski and designated a neotype for *H. calcaratus* (C.L. Koch, 1839), the type species of genus *Holoparasitus*.

During the last decade new taxa have been identified in the course of faunistic and ecological programs or from acarological collections (Schmölzer, 1991, 1995a, 1995b; Vinnik, 1994; Witaliñski, 1994a, 1994b; Juvara-Bals, 1995). As mentioned above, *Holoparasitus* s. str. includes now 30 species. Unfortunately, some of these

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species are known incompletely (one sex only) and their descriptions frequently lack details. This rather large subgenus strongly requires a phylogenetical analysis. However, it cannot be successfully done until the following problems are still unsolved:

- the revision of the species deposited in the collections of the Berlese, v. Vitzthum and Willmann;
- the re-examination of some key morphological characters omitted in early descriptions in some species;
- a more complete documentation about the gamasid mites in many European regions, especially those from south-east and central Europe, is available.

The aim of this paper is to advance the knowledge of species included in the subgenus *Holoparasitus* s. str. as defined in Juvara-Bals (1975). A revision of specimens labelled as *H. apenninorum* (Berlese, 1906) in the Berlese collection ("Berlese Acaroteca", Florence, Italy) showed that this is a complex of four species: one of them we have identified as the nominal species while the three others are new species. We also describe two additional new species from Spain and Sicily, *H. gibber* sp. n. and *H. ellipticus* sp. n., respectively. These latter species form together with *H. siculus* (Berlese, 1905), *H. mallorcae* Juvara-Bals, 1975, *H. lawrencei* Hyatt, 1987 and *H. maritimus* Hyatt, 1987, a well defined group of species which we named *mallorcae*-group. Additionally, we redescribe the male of *H. cultriger* (Berlese, 1906) based on the single type specimen in the Berlese Acaroteca.

MATERIAL AND METHODS

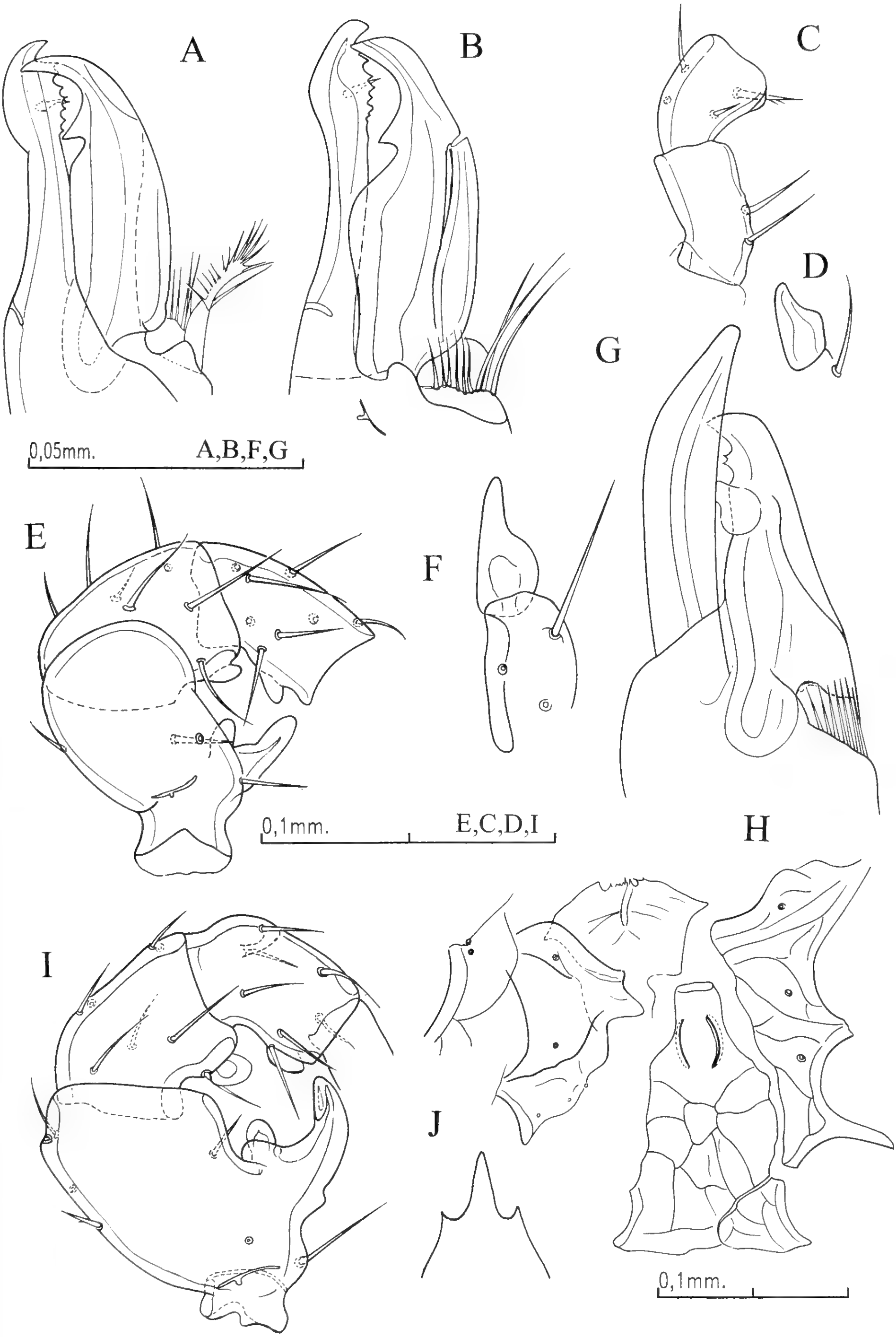
The material comes from Italy and Spain. One of us (WW) was provided with a large collection of samples from Italy collected by Prof. R. Dallai and the staff of the Department of Evolutionary Biology, University of Siena, Italy (DEBS). Juvara-Bals had the opportunity to identify samples of mites (family Parasitidae) from Italy (Toscana) collected by Dr. F. Pegazanno and Dr. R. Nannelli from the Experimental Institute of Agricultural Zoology (EIAZ), Florence, Italy. She was also working on the genus *Holoparasitus* from the Athias-Henriot collection deposited in the Museum of Natural History (MHNG), Geneva, Switzerland.

We studied material from the Berlese Acaroteca (EIAZ) which contains several species collected generally around Florence (Toscana) and in Umbria.

Morphological terminology follows mainly Evans and Till (1979) and Van der Hammen (1980). Setal notation for the idiosoma follows Lindquist and Evans (1965). Measurements were made from slide-mounted material and expressed in micrometers (µm). The types are deposited in the Zoological Museum of the Jagiellonian University, Cracow, Poland (ZMJU), in the MHNG and in the EIAZ.

FIG. 1

Holoparasitus apenninorum (Berlese,1906). Male: A- chelicera, paraxial view; B-idem, antiaxial; C-pedipalp, trochanter and femur; D-corniculus; E-leg II, femur, genu and tibia.
H. cultriger (Berlese,1906). Male: F-corniculus; G-chelicera, paraxial; H-sternogenital region and genital lamina; I-leg II, femur, genu and tibia; J-tectum (after Berlese, 1906).


A
B
C
D
G
0,05mm. A,B,F,G
E
F
0,1mm. E,C,D,I
H
I
J
0,1mm.

SYSTEMATIC ACCOUNT

REVISION OF *HOLOPARASITUS APENNINORUM* (BERLESE, 1906) AND *H. CULTRIGER* (BERLESE, 1906)

The material of *H. apenninorum* (Berlese, 1906) in the Berlese collection named *Ologamasus pollicipatus* var. *apenninorum* consists of 28 specimens on 10 slides and is in fact a mixture of four species, i.e.:

1. *H. apenninorum* (Berlese, 1906), 1♂ non-dissected (slide 5/19), Vallombrosa (Toscana, Italy), from moss; lectotype by present designation.

2. *H. crassisetosus* sp. n., 1♀ dissected (6/40), 4♀♀ (6/41), 6♂♂, 1♀, 2 deutonymphs (7/35), 2♂♂, 2♀♀ (7/37), Vallombrosa.

3. *H. digitiformis* sp. n., 1♀ (6/42), 1♂ (6/43), 1♀ (6/44), Monte Senario (Toscana).

4. *H. cornutus* sp. n., 1♂, 1♀ (7/39), Bevagna (Umbria, Italy); 1♂, 3♀♀ (7/40), Monte alle Forche (Toscana).

Berlese also recognized in his material from Vallombrosa another variety, *Ologamasus pollicipatus* var. *cultriger*. This is a valid species, *Holoparasitus cultriger* (Berlese,1906), though only one specimen is known, a dissected male which is on slide 5/19 together with the lectotype of *H. apenninorum* noted above. Some specimens of *Paragamasus decipiens* (Berlese, 1903) and of *Holoparasitus* mentioned above are mounted together: 1♀ on slide 6/44, 1♀ on slide 7/39 and 1♂, 1♀ on slide 7/40.

H. apenninorum (Berlese, 1906) Fig. 1 A-E

Gamasus (Ologamasus) pollicipatus var. *apenninorum* Berlese, 1906: 253 (in part).
Holoparasitus lichenis var. *apenninorum* (Berlese, 1887) sensu Turk 1953, Micherdziñski 1969: 372.
not *Holoparasitus apenninorum* (Berlese, 1906) sensu Juvara-Bals 1975, Acarologia, p: 400.

Type material: lectotype 1♂ non-dissected, slide 5/19, from moss, Vallombrosa (Toscana) in Berlese Acaroteca, EIAZ; by present designation.

Our description is based on a non-dissected single male in lateral position so that only some of the main characters could be observed.

Diagnosis. Male: excipulum absent; cheliceral movable digit with a single tooth, fixed digit enlarged along its distal third, with 6-7 denticles; leg II with the femoral apophysis straight and thumb-like (Fig. 1E).

Description. Male. The legs I-IV were attached only on the right side of the animal. The others were lost but leg II could be seen in the mounting medium detached from the animal. Gnathosoma. Movable digit of chelicera with a single tooth situated medially. Fixed digit, enlarged along its upper third, with 6-7 denticles. Spermatotreme in the form of a fine slit, arthrodial process setiform antiaxially and brush-like paraxially (Fig. 1 A,B). Pedipalp: trochanter simple, femur with slight ventral protuberance located distally (Fig. 1 C). Corniculi triangular, with small protuberance on ventral side (Fig. 1 D).

Leg II. Main features of leg II shown in figure 1 E. Femoral apophysis straight and thumb-like, axillary process elongated and smooth. Spur on genu and tibia conical, located midway on ventral face. Measurements: tarsus I = 104 µm; tarsus IV = 122µm.

Discussion. Berlese's (1906) original description of *H. apenninorum* was based on a male and several females, from a moss sample taken at Vallombrosa. Berlese described in detail only the male's chelicera but presented figures of three different chelicerae as well as of the epistome, and of the male's leg II. The drawing of the chelicera shown in the fig. 15a, tab. XIII. (♂ from Vallombrosa) corresponds to the original description which specified that "digitus mobilis basi latiusculus, externe gibbosus, dente magno, unico..."; the characteristics of this type of chelicera can be seen only on the non-dissected male of the slide 5/19. Berlese attributed to *H. apenninorum* two other chelicerae (Fig. 15, Fig. 16, tav. XIII) which have two teeth on the inner margin of the digitus mobilis. He also mentioned a figure 16a which in fact does not exist. Micherdziñski (1969) paid also attention to the similarity between Berlese's initial description and only one of the chelicerae illustrated. Berlese's figure of the male's leg II corresponds either to the leg of *H. digitiformis* or to that of *H. crassisetosus*, two species found in the same area as *H. apenninorum*. The triangular epistome figured by Berlese can not be seen any more because of the lateral position of the animal.

The characteristics of the female endogynium was neither described nor drawn in detail; figure 7, tab. XIX refers either to *H. digitiformis* or to *H. crassisetosus* which have very similar females. Berlese's material also contained *H. crassisetosus* from Vallombrosa and *H. digitiformis* from Monte Senario. Unfortunately, we did not find another male of *H. apenninorum* or a corresponding female. However, it is obvious that the male mounted on slide 5/19 is a syntype. We designate it as the lectotype of *H. apenninorum* (Berlese, 1906).

Specimens identified by Juvara-Bals (1975) as *H. apenninorum* belongs in fact to *H. cornutus* sp. n. The species was misidentified because at that time it was not recognized that original description of Berlese related to a mixture of species.

H. cultriger (Berlese, 1906) Fig. 1 F-J

Type material: 1♂ holotype, dissected (slide 5/19), Vallombrosa (Toscana, Italy), from moss, Berlese Acaroteca (EIAZ).

Diagnosis. Male: excipulum present; cheliceral movable digit with two little denticles, fixed digit markedly longer than movable one, blade-like and toothless; leg II with tibia bearing two processes: dorsally one rounded located near proximal margin and ventally an elongated situated near distal margin (Fig. 1 I).

Description. Male. The length of the idiosoma could not be measured because the single specimen is in pieces. The few characteristics observed are shown in figure 1. Sternogenital region reticulated, with slightly sclerotized excipulum; anterior margin of genital lamina with several small denticles in the middle (Fig. 1 H).

Gnathosoma. Tectum trispinate, central prong well developed (Fig. 1 J). Corniculi triangular, each with ventral protuberance (Fig. 1 F). Chelicera as in figure 1 G:

fixed digit blade-like and toothless, markedly longer than movable one; movable digit with two little denticles subapically.

Legs. Armature of legs II as in figure 1 I. Femoral apophysis strong, thumb-like and curved; axillary process short and rounded. Genual process large, plump or rounded, situated in distal half on ventral face. Tibia with two protuberances: regular process elongated and located ventrally close to distal margin of segment, an extra process larger, located dorsally on proximal third of segment. Ventral face of trochanter IV with protuberance. Measurements: tarsus I = 138 µm, tarsus IV = 150 µm.

Discussion. Berlese described this species on the basis of a single male in poor condition. The type specimen is together with that of *H. apenninorum* on the same slide. The two types may be easily distinguished: *H. apenninorum* is in lateral view and non-dissected while *H. cultriger* is in several pieces. The most valuable character separating *H. cultriger* from the other species with an excipulum is the special blade-shaped fixed digit of the chelicera.

Holoparasitus crassisetosus sp. n. Figs. 2,3

Type material: 1♂ holotype, 48♂♂, 66♀♀ paratypes, Vallombrosa (Toscana, Italy) (alt. 960 m), coniferous forest (*Abies alba*), 6.11.1982. Collected by the staff of DEBS. The holotype as well as 4♂♂ and 5♀♀ paratypes have been deposited in MHNG, 44♂♂ and 61♀♀ have been deposited in ZMJU.

Other material examined: Berlese Acaroteca (EIAZ), 1♀ (slide 6/40), 4♀♀ (6/41), 2♂♂, 2♀♀ (7/37), 5♂♂, 2♀♀, 2 deutonymphs (7/35). All this material was collected in Vallombrosa, but the habitat was not specified.

Diagnosis. The species is recognisable by very thick seta pv1 on tibia IV in both sexes (Fig. 2 A,B).

Description. Male. Idiosoma brown, well sclerotized. Dimensions of idiosoma: 555-585 x 365-380 µm; L/W (length/width) factor 1.46-1.56, N=10. Podonotal region with 20 pairs of setae, j1 = 38-40 µm, other 19-22 µm; opisthonotal region with 30 pairs of shorter setae, 10–13 µm.

Ventral side (Fig. 2 C). Genital lamina large, located in a well sclerotized concavity, its lateral sides forming triangular sharp projections, its anterior edge with median pleated membrane and two lobes; postero-lateral edges of genital lamina with two well sclerotized protrusions.

Male genital orifice, flanked by triangular presternal shields and provided with large rectangular microsclerite bearing tritosternum. Reticulation of sternogenital region regular; between anterior margin and close to sternal setae 1 (st1), sternal shield more heavily sclerotized and its reticulation slightly convex; length of sternal setae about 42 µm. Opisthogastric region with 8 pairs of setae (26-39 µm).

Gnathosoma. Tectum trispinate, with long, broad central prong (Fig. 3 I). Corniculi with paraxial margin forming rounded lamellar protrusion (Fig. 2 D,E). Hypognathal groove with 11 complete rows of denticles; palpcoxal setae pilose, hypostomatic setae simple (Fig. 2 D). Chelicera (Fig. 2 F,G). Both digits short and robust. Fixed digit toothless, with pilus dentilis flanked by two convex laminae. Movable digit with two teeth. Arthrodial membrane at the base of movable digit with well developed

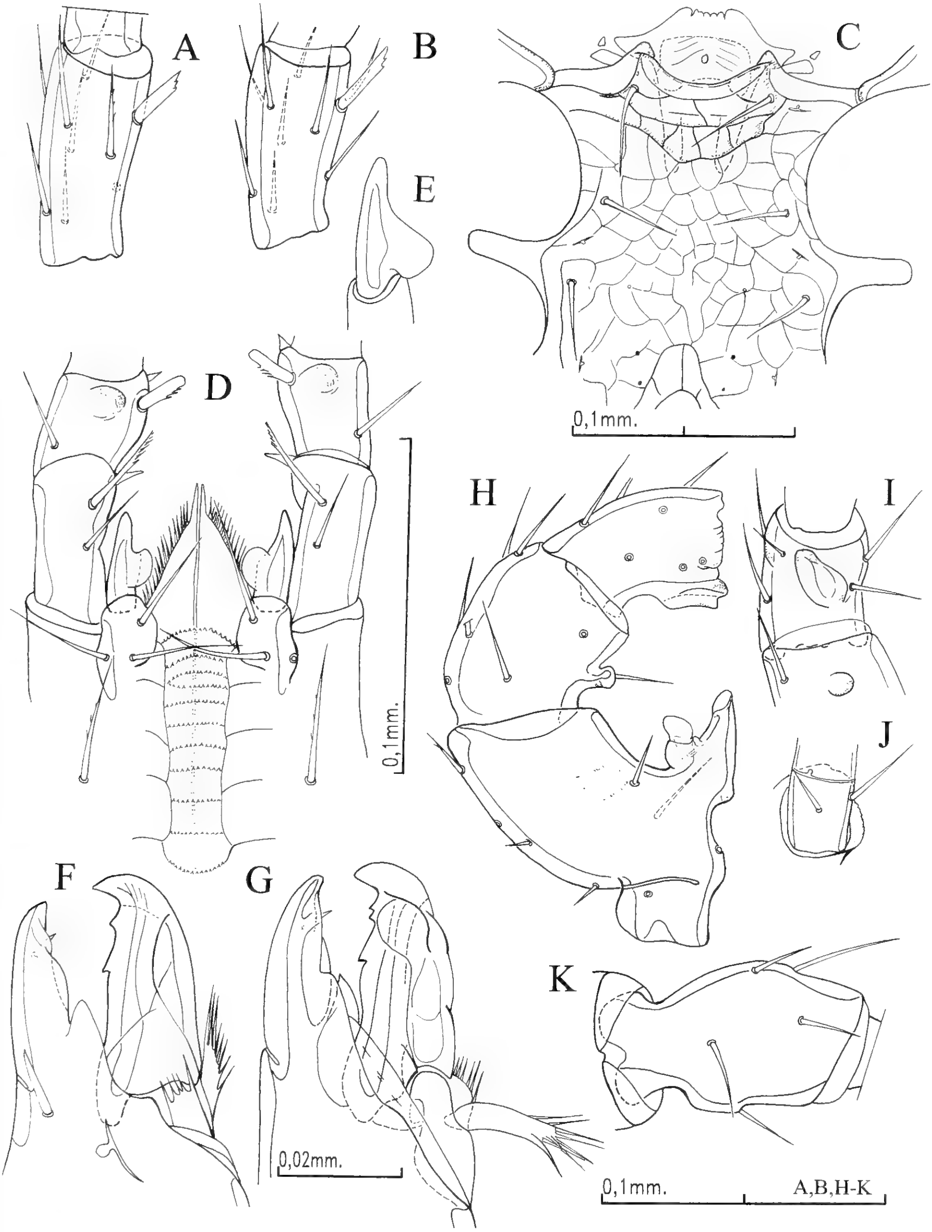


FIG. 2

Holoparasitus crassisetosus sp. n. Male: A-tibia IV; C-sternogenital region and genital lamina; D-gnathosoma, palptrochanter and palpfemur; ventral; E-corniculus; F-chelicera, antiaxial; G-idem, paraxial; H-leg II, femur, genu and tibia, antiaxial; I-tibia, ventral; J-basis tarsus and cuticular edge of tibia; Female: B-tibia IV.

brush-like process on paraxial side and a lesser developed one on antiaxial side, synarthrodial membrane short and wedge-shaped.

Pedipalps. Trochanter with proximal seta (v1) simple and distal seta (v2) pilose. Femur with tubercle located on ventral side close to anterolateral seta. Anterolateral seta of femur spatulate and pectinate on inner side (Fig. 2 D); anterolateral setae of genu spatulate.

Legs. Coxae II with ridge of 5 denticles (Fig. 3 J). Leg II armed as shown in figure 2 H-I. Femoral apophysis finger-shaped and straight, axillary process curved towards the femur. Spur on genu small, round, located ventrally in the middle. Apophysis on tibia low and long, with slightly convex margin, attached ventrally and reaching with its rounded distal end the margin of segment; the cuticle of anterodistal edge of tibia with several fine furrows. Trochanter IV with flattened protuberance situated medioposteriorly (Fig. 2 K). On tibia IV seta pv1 conspicuous, very thick with a dentate end (Fig. 2 A). Measurements: tarsus I = 139-144 μm; tarsus IV = 146μm.

Female. Idiosoma brown, well sclerotized. Dimensions of idiosoma: 630-665 x 445-475μm (L/W factor 1.36-1.45, N=10). Podonotal setae: j1 = 39 μm, other setae 19-26μm; opisthonotal setae 12-18 μm.

Ventral side (Fig. 3 A). Fused presternal shields forming smooth ribbon, partially connected to lateral platelets. Anterior margin of sternal plate sometimes with incisions of a soft cuticle, laterally to setae st1. Reticulation of sternal shield with two prominent lines delimiting a slightly more sclerotized anterior region of sternum: one line V-shaped extending medially and second line running close to second pair of pores (pst2). Margin of exopodal plate facing coxa I sclerotized.

Genital region. Epigynial plate heptagonal, anterior margin with a middle triangular apex and two lateral spines curved antiaxially; subapical structure small and oval, with lateral rounded protrusions extending beyond epigynial margin (Fig. 3 C). Paragynia rectangular with elliptical thickenings in front of coxae IV and not extending beyond paragynium edge, paragynial posterior protrusions elongated (Fig. 3 B). Endogynium oval, 22 x 29 to 24 x 31 μm. Distance between endogynial margin and coxa IV nearly two times larger than endogynium length (56-59 μm). Shape of endogynium cup-like, with anterior margin protruding into dorsally directed appendage, which looks like hollow tube (Fig. 3 D). Gland pores behind coxa IV large. Opistho-gastric region with 8 pairs of setae, their length 36-39 μm.

Gnathosoma. Tectum trispinate, central prong long and narrow, lateral prongs small; minute additional spines discernible between central and lateral prongs (Fig. 3 E). Corniculi conical. Hypognathal groove with 6-8 rows of denticles ending at palpcoxal setae level; some lateral lines present, starting from hypognathal groove; cuticular ridges between palpcoxal setae serrated (Fig. 3 F). Palpcoxal setae slightly pilose, hypostomatic setae simple.

Chelicera. Fixed digit with two teeth in front of pilus dentilis, a third, smaller tooth frequently present between them; two teeth and a lamella with slightly concave edge located behind pilus dentilis. Movable digit with three teeth (Fig. 3 G).

Pedipalps. Proximal seta of trochanter (v1) simple, distal seta (v2) pilose (Fig. 3 F), anterolateral seta of femur spatulate and pectinate on one side, and anterolateral setae of genu spatulate. Femur with poorly visible tubercle located anterolaterally.

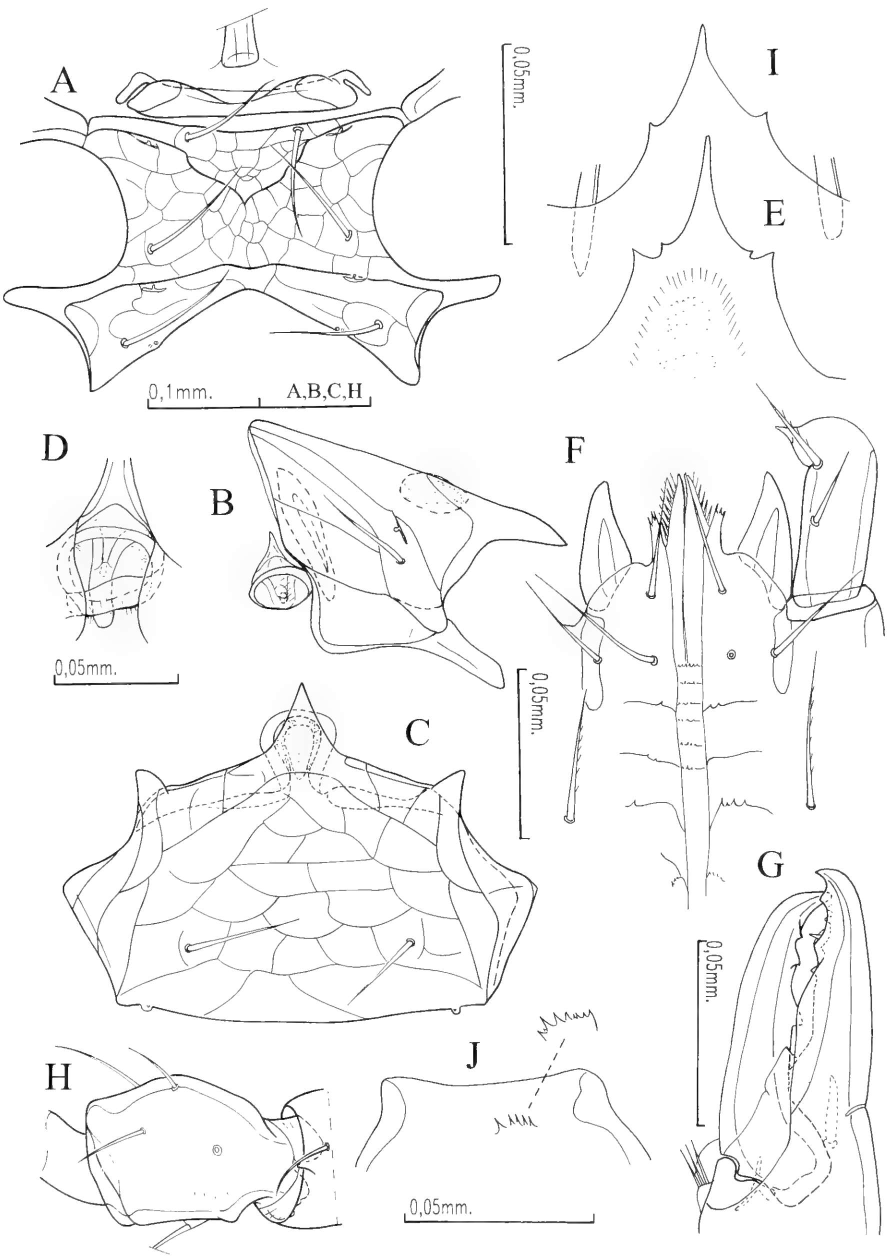


FIG. 3

Holoparasitus crassisetosus sp. n. Female: A-presternal and sternal shields; B-paragynium; C-epigynium; D-endogynium; E-tectum; F-gnathosoma and palptrochanter, ventral; G-chelicera, paraxial; H-trochanter IV, ventral. Male: I-tectum; J-coxa II, denticulated ridge.

Legs. Coxa II with a ridge of about 5 denticles on anterior face. Tibia IV with very thick pv1 seta, its end dentate (Fig. 2 B). Trochanter IV with rounded protuberance located on proximal third of posterior face (Fig. 3 H).

Measurements: tarsus I = 144-154 µm; tarsus IV = 156-163 µm.

Discussion. Males and females of *H. crassisetosus* are very similar to those of *H. digitiformis*. From other *Holoparasitus* species known to date these species differ in the following features. In males, excipulum is absent, tectum trispinate, movable and fixed digits of chelicera with 2 and 0 teeth, respectively. Corniculi posses a lamellar dilatation or indentation on the paraxial margin. In females, presternal plates and lateral platelets accreted, the endogynium soup-spoon-shaped. The most easily recognized feature which distinguishes *H. crassisetosus* and *H. digitiformis* is the presence of the transformed pv1 seta of tibia IV in both sexes of the former species. A detailed discussion of the most important differences between the two species is given at the end of the description of *H. digitiformis*.

Holoparasitus digitiformis sp. n. Figs 4, 5

Type material: 1♂ holotype, 52♂♂, 39♀♀ paratypes, from litter of oak forest (*Quercus cerris*, *Q. pubescens*) and 68 ♂♂ and 72♀♀ paratypes, from litter of pine forest (*Pinus nigra*, *Erica arborea*, *Juniperus communis*). The two forests are situated at Selvapiano (Commune di Rufina, Toscana), 25 km away from Florence at an altitude of 200 m. The two habitats are about 300 m apart and are situated on the same side of the mountain, facing south-west. The material was collected from February 1971 to April 1974 by Dr. R. Nannelli and Dr. F. Pegazzano (EIAZ).

Other material examined: 19♂♂, 15♀♀, Catena del Marghine (Marghine Range), Sardinia, from moss and lichens in yew (*Taxus baccata*) and oak forests along the road to Bolotana, alt. ca 1000 m, 30.03.1977, collected by the staff of the DEBS and deposited in ZMJU.

1♀ (slide 6/42), 1♂ (6/43), 1♀ (6/44), Monte Senario, Toscana, Berlese Acaroteca (EIAZ). The material has been deposited as follows: 1♂ holotype, 32♂♂, 19♀♀ paratypes from oak forest and 48♂♂, 52♀♀ paratypes from pine forest – in MHNG; 20♂♂, 20♀♀ paratypes from both habitats - in ZMJU; 20♂♂, 20♀♀ paratypes from both habitats - in EIAZ.

Diagnosis. In both sexes all setae on tibia IV of normal appearance. Male: excipulum absent; movable digit of chelicera with two denticles, fixed digit edentate, slender, finger-like, with slightly dilated apex. Female: epigynium with subapical small ovoid microsclerite and hyaline wing-like protrusions extending anterolaterally (Fig. 5 D). Endogynium small, oval, inverted cup-like, with anterior margin protruding into a cuticular solid appendage directed more or less dorsally (Fig. 5 B,C,E).

Description. Male. Idiosoma well sclerotized. Dimensions of idiosoma: specimens from Selvapiano, Toscana, oak forest: length 576-617 µm; idem, specimens from pine wood, length 634-641 µm. Specimens from Sardinia, idiosoma size 585-635 x 405-430 µm (L/W factor 1.45-1.57, N=10). Podonotal region with 21 pairs of seta, j1=39 µm, the others 26-28 µm opisthonotal region with about 30 pairs, 19-24 µm.

Ventral side. Genital lamina large, situated in well defined concavity of heavily sclerotized anterior margin of sternal shield; anterior margin of the lamina with two fine lobes separated by a concavity and two lateral triangular prongs. Between lateral prongs and anterior lobes, on their inner face, two well sclerotized prominences. Behind genital lamina a rectangular microsclerite with a rounded lobe ventrally supporting the base of

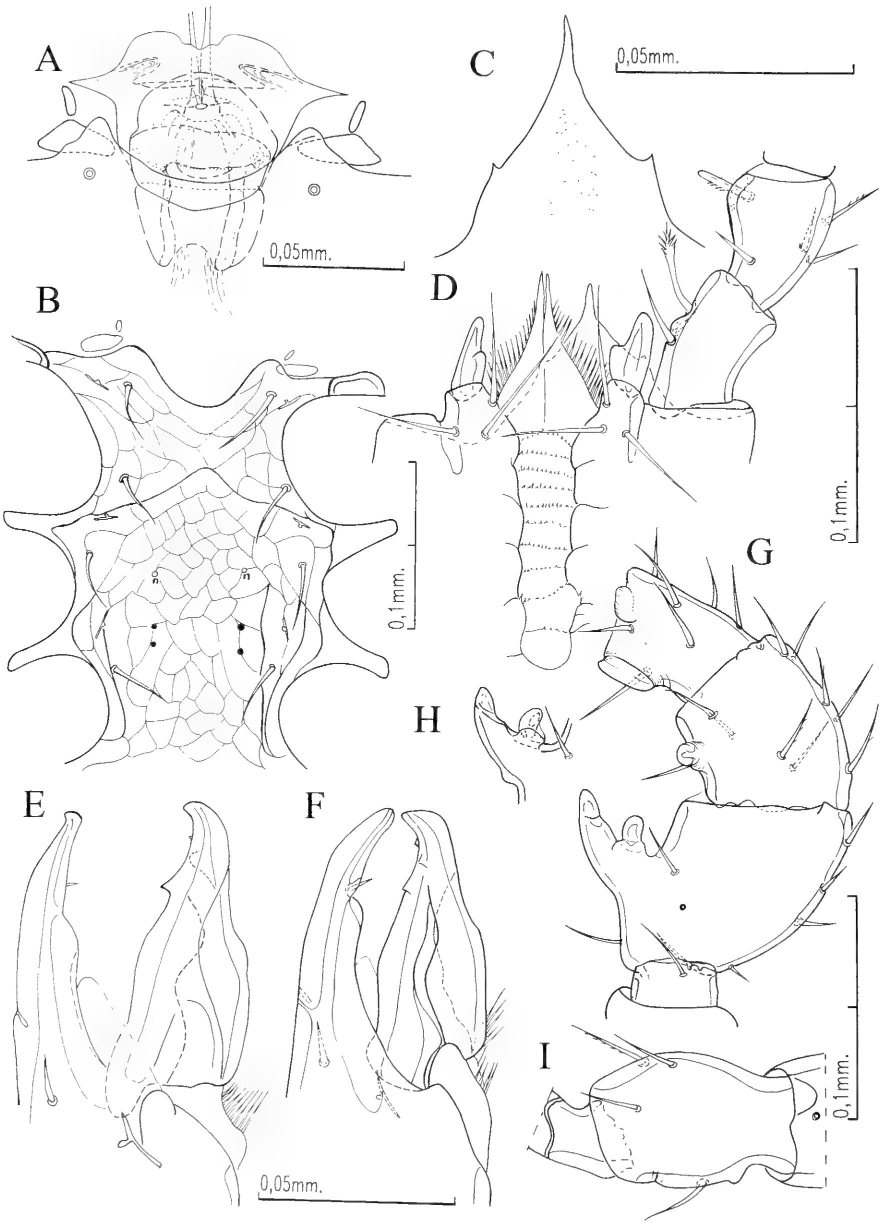


FIG. 4

Holoparasitus digitiformis sp. n. Male: A-genital lamina; B-sternogenital shield; C-tectum; D-gnathosoma and palptrochanter, palpfemur, ventral; E-chelicera; F-idem, paraxial; G-leg II, femur, genu and tibia, paraxial; H-femoral apophysis, antiaxial; I-trochanter IV, ventral.

tritosternum (Fig. 4 A). Sternogenital shield with scale-like reticulation and with marked line (inverted V) behind second pair of sternal setae; length of sternal setae 39-46 µm (Fig. 4 B). Large gland pore behind coxae IV. On opisthogaster 8 pairs of setae, 24-36 µm.

Gnathosoma. Tectum trispinate, lateral prongs small, the central one large, broad at the base and pointed (Fig. 4 C). Corniculi with small prominence situated paraxially; hypognathal groove with 10-11 rows of denticles; palpcoxal setae finely pilose, hypostomatic setae simple (Fig. 4 D).

Chelicera (Fig. 4 E,F). Fixed digit edentate, slender, finger-like; its apex slightly dilated and sometimes curved. Movable digit with two denticles, the distal one sometimes appearing much more paraxially, synarthrodial membrane rounded. Spermatodactyl large, with a median concavity; arthrodial membrane with short brushy process paraxially and setiform margin antiaxially.

Pedipalps. Palptrochanter with seta v1 thin and simple, whereas v2 thicker and pilose. Palpfemur with anterolateral seta pectinate on one edge; palpgenual anterolateral setae simply spatulate. Palpfemoral segment swollen distally, with tubercle located on ventral side, close to al seta (Fig. 4 D).

Legs. Coxa I with a ridge bearing 6-7 denticles, situated paraxially close to distal margin. Coxa II with ridge of 8-10 denticles (Fig. 5 J). Armature of leg II illustrated in figure 4 G.

Femoral apophysis relatively long, finger-shaped, with curved apex and a small tubercle on its base (Fig. 4 H); axillary process curved. Genu with small rounded spur situated medioventrally. Tibia with two spurs: one low and elongated, reaching distal margin, another smaller, located anterolaterally and extending beyond segment margin. Posterior face of trochanter IV with a small tubercle under seta pv (Fig. 4 I).

Measurements: specimens from Toscana: tarsus I = 156-158 µm; tarsus IV = 168-173 µm.

Female. Idiosoma well sclerotized, brown coloured. Dimensions of idiosoma: 660-710 x 490-530 µm (L/W factor 1.28-1.42, N=10). Podonotal region with 21 pairs of setae, j1=36µm, the others 16-20 µm; opisthonotal region with 33 pairs of short setae (13-16 µm).

Ventral side. Accreted presternal shields forming a smooth ribbon-shaped plate, more narrow medially; lateral presternal platelets usually free. Anterior margin of sternal plate with two less sclerotized concavities, frequently flanking bases of setae st1; reticulation of sternum easily discernible with prominent arched transverse line passing close to pores pst2 (Fig. 5 A); length of sternal setae from 46 µm (st1) to 65 µm (st3). Anterior edge of exopodal shield facing leg I thickened.

Genital region. Paragynial shield with sclerotized elliptical thickening in front of coxa IV (Fig. 5 B,C). Postero-lateral protrusions long and narrow, ending with rounded or sometimes pointed edge. Metagynial sclerites with paraxial margins convex. Epigynial shield with anterior margin formed by a triangular central apex and two large lateral prongs curved antiaxially; subapical epigynial structure with small ovoid microsclerite and hyaline wing-like protrusions extending anterolaterally (Fig. 5 D). Endogynium (Fig. 5 B,C,E) small, oval (20 x 27 µm to 27 x 33 µm), inverted cup-like,

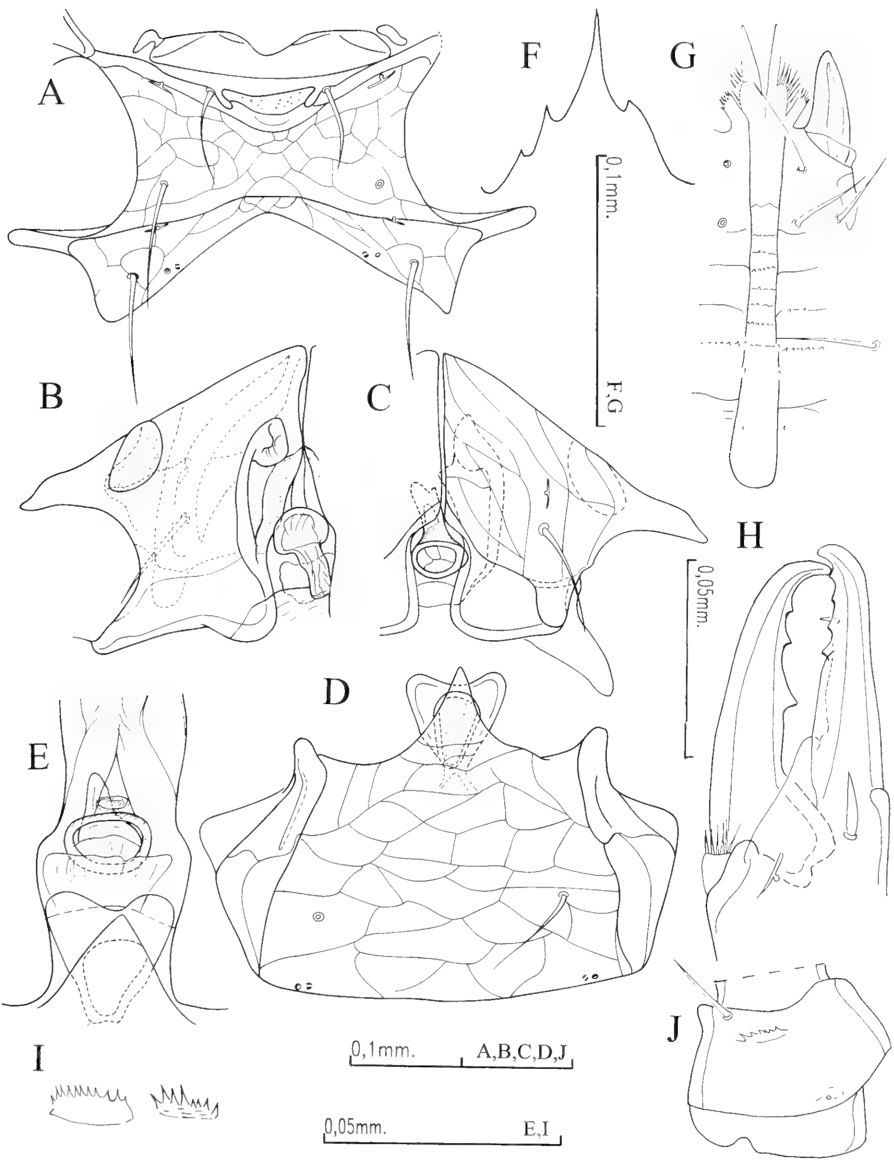


FIG. 5

Holoparasitus digitiformis sp. n. Female.: A-presternal and sternal shields; B-paragynia and endogynium, dorsal; C-idem, ventral; D-epigynium; E-endogynium; F-tectum; G-hypognathal groove and corniculus; H-chelicera, antiaxial; I-coxa II, denticulated ridge. Male: J-coxa II, paraxial.

with anterior margin protruding into a cuticular solid appendage directed more or less dorsally; poorly visible scale-like fine hyaline flap covering endogynium on ventral side. Gland pores behind coxa IV large. Opisthogastric region with 8 pairs of setae, their length about 39 μm.

Gnathosoma. Tectum usually trispinate, with central prong sharply pointed, sometimes an extra spine present on one side (Fig. 5 F). Corniculi conical. Hypognathal groove with 8-11 rows of denticles, those located posterior to the level of palpcoxal setae frequently reduced or absent, some lateral lines present between hypostomatics and palpcoxal setae (Fig. 5 G). Palpcoxal setae pilose, hypostomatics simple.

Chelicera. Fixed digit with two teeth in front of pilus dentilis, two more teeth and a thin, concave cuticular edge behind pilus dentilis. Movable digit with three teeth (Fig. 5 H).

Pedipalps. Trochanter ventral setae finely pilose; anterolateral seta of femur spatulate and pectinate on one edge; anterolateral setae of genu simply spatulate. Palpfemur swollen distally, with tubercle located on ventral side close to anterolateral seta.

Legs. Leg structure and setation unremarkable. Coxa I with row of about 10 little denticles on distal paraxial margin. Coxa II with ridge of 8 to 10 fine denticles situated on anterior face (Fig. 5 I). Measurements: tarsus I = 154-163 μm; tarsus IV = 168-175 μm.

Discussion. H. digitiformis is similar to *H. crassisetosus* in respect to the general structure of the genital region in the female and to the shape of the armature of leg II in the male.

The endogynium in both species is small and inverted cup-shaped, with the anterior margin forming a cuticular protrusion directed dorsally, thus similar in appearance to a soup-spoon. In *H. crassisetosus*, this protrusion is relatively shorter (as compared with the size of endogynium) than in *H. digitiformis* and appears as a hollow tube. The metagynial sclerites are oriented roughly parallel in both species, but in *H. digitiformis* their lateral margins are convex, whereas in *H. crassisetosus* they are rather concave. The subapical epigynial structure has prominent wing-like protrusions in *H. digitiformis* but only small round protrusions in *H. crassisetosus* .

Males in both species have a very similar armature of leg II, especially on the femur and genu; on the tibia, however, in *H. digitiformis* the additional prominent anterolateral tubercle is present, whereas in *H. crassisetosus* the cuticle of corresponding place shows fine furrows only. A very pronounced difference can be seen in the shape of the male corniculi: *H. digitiformis* has a small protuberance on the paraxial margin, whereas in *H. crassisetosus* this margin extends prominently forming a thin rounded lamella.

In both sexes, the most important character for differentiation of these two species remains the form of seta pv1 of tibia IV: it is narrow and simple in *H. digitiformis* but thick and notched at the end in *H. crassisetosus*. *H. digitiformis* was found in the surroundings of Florence (Toscana) in coniferous forest as well as in Sardinia where it occurs in soil of yew and oak forests. *H. crassisetosus* was collected, till now, only from Vallombrosa (Toscana), where it lives in coniferous forests.

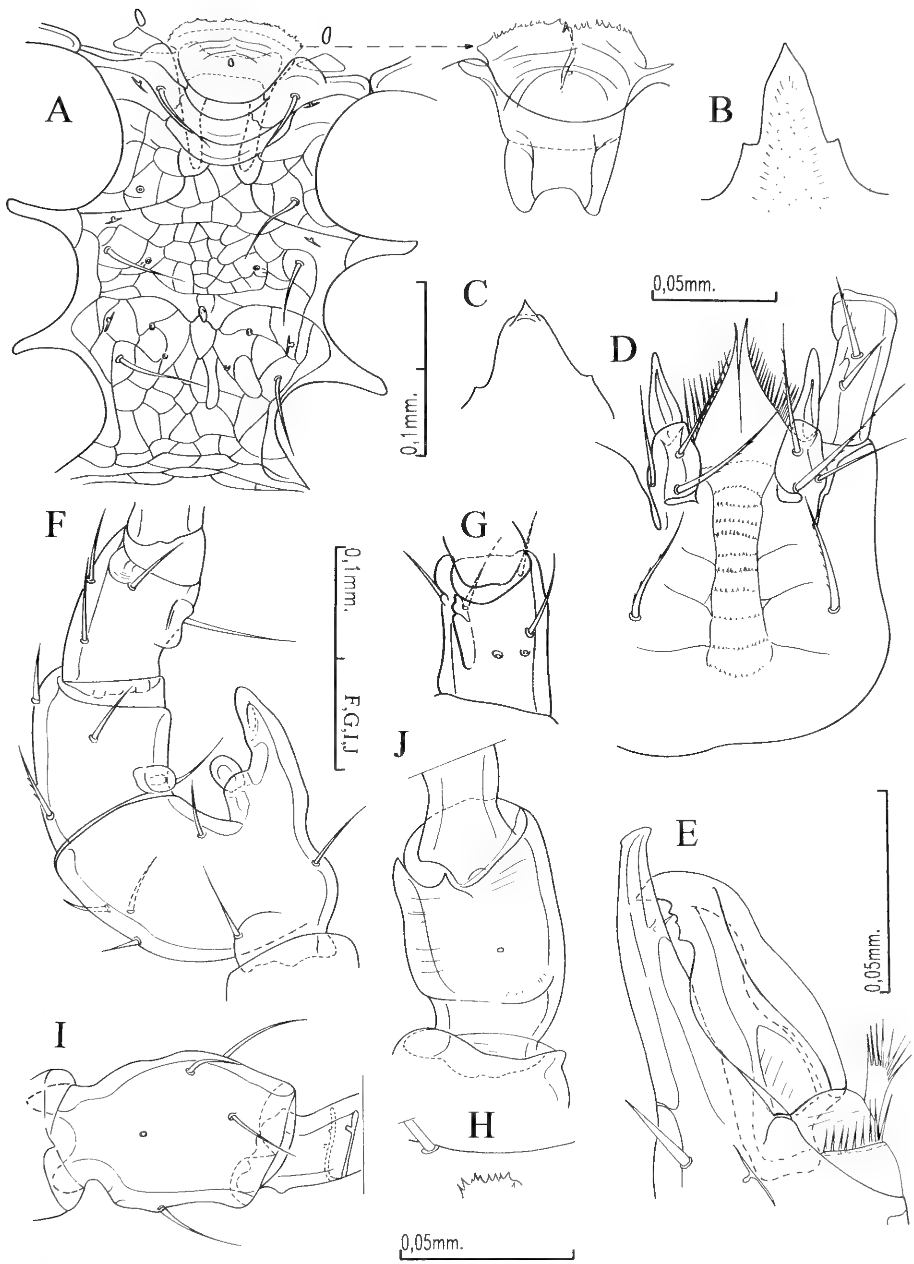


FIG. 6

Holoparasitus cornutus sp.n. Male: A-scutum sternogenital and genital lamina; B-tectum; C-tectum (Bevagna-Umbria, Berlese Acaroteca); D-gnathosoma and palptrochanter, ventral; E-chelicera, antiaxial; F-leg II, femur, genu and tibia; G-tibia II, ventral (Bevagna-Umbria, Berlese Acaroteca); H-coxa II, denticulate ridge; I-trochanter IV, ventral; J-idem, dorsal.

Holoparasitus cornutus sp. n. Figs. 6, 7

H. apenninorum sensu Juvara-Bals 1975: 400; nec Berlese, 1906.

Type material: 1♂ holotype, 2♂♂, 4♀♀ paratypes, Vallombrosa (Toscana, Italy), litter in beach forest, 19.09.1971; 14♂♂, 11♀♀ paratypes, Vallombrosa, moss in coniferous forest (*Abies alba*), alt. 960 m, 6.11.1982. All paratypes collected by the staff of DEBS. The holotype and 1♂, 2♀♀, 2 deutonymphs have been deposited in MHNG, whereas 16♂♂, 13♀♀ in ZMJU.

Other material examined. Italy: 1♂, 1♀, Monte Amiata near Siena, Toscana, litter in beach forest, alt. ca. 900 m; 4♀♀, Monte Amiata, litter in chestnut forest, alt. ca. 800 m, 17.09.1990, leg. W. Witaliñski, deposited in ZMJU. 1♂, 3♀♀ (slide 7/40), Monte alle Forche, Toscana, and 1♂, 1♀ (slide 7/39), Bevagna, Umbria, Berlese Acaroteca (EIAZ).

Romania: 1♂, 1♀, Cerbului Valley, Busteni, Bucegi Mountain, Meridional Carpathians, sawdust and litter, beech and spruce forest, 5.6.1967, leg. I. Juvara-Bals, deposited in MHNG.

Diagnosis. The species can be recognized by a lamellar process ending with one or two spurs, situated more or less dorsally at the distal margin of trochanter IV in both sexes. Male: excipulum absent; two incisions in sclerotized cuticle behind each group of hypostomatic setae; folded cuticle at the level of legs IV. Female: endogynial sack rounded, with two large, connected teeth on each side .

Description. Male. Idiosoma well sclerotized, its dimensions (Italy) 672-715 x 452-510 µm (L/W factor 1.42-1.48, N=5). Podonotal setae: j1=38 µm, other setae 20-26 µm; opisthonotal setae shorter, 13-19 µm.

Ventral side (Fig. 6 A). Genital lamina with serrated anterior margin. Sternal shield reticulated with a slight median prominence distally; two ridges run from this prominence posteriorly to sternal setae st2 towards the margin of the shield. At the level of coxa IV, cuticle folded in a strongly sclerotized line. Length of sternal setae from 48 µm (st1) to 40 µm (st3). On opisthogastric region 8 pairs of setae, their length from 42 µm (Jv1) to 26 µm (Jv5).

Gnathosoma. Tectum trispinate with central prong triangular, long, and in the specimen from Bevagna, with a little denticle on its tip; lateral prongs tiny (Fig. 6 B,C). Hypognathal groove provided with 11 well dentated rows; gnathosomal setae pilose, except simple hypostomatic seta 3. Behind hypostomatic setae there are incisions in sclerotized cuticle (Fig. 6 D). Corniculi conical. Chelicera (Fig. 6 E). Fixed digit edentate and with truncate apex; movable digit with 2-4 small subapical teeth. Arthrodial membrane formed by a short brush-like processes paraxially and a setiform fringe antiaxially.

Pedipalps. Palptrochanter with seta v1 simple and v2 pilose; palpfemur with distal protuberance on its ventral face.

Legs. Coxa II with ridge bearing 9 denticles located on anterior face (Fig. 6 H). Armature of leg II shown in figure 6 F. Main femoral apophysis long, finger-like, its axillary spur rounded. Spur on genu rounded. Tibia with median saddle-like spur and little distal protuberance situated anterolaterally (Fig. 6 F,G). Dorsal or posterodorsal face of trochanter IV with distal lamellar process ending with one or two spurs; proximal posterolateral face with a protuberance (Fig. 6 I,J). Gland pores behind coxae IV located in a normal cuticle. Measurements: tarsus I = 143 µm (specimen from Romania) and 173-177 µm (specimens from Italy); tarsus IV = 173 µm (Romania) and 184-193 µm (Italy).

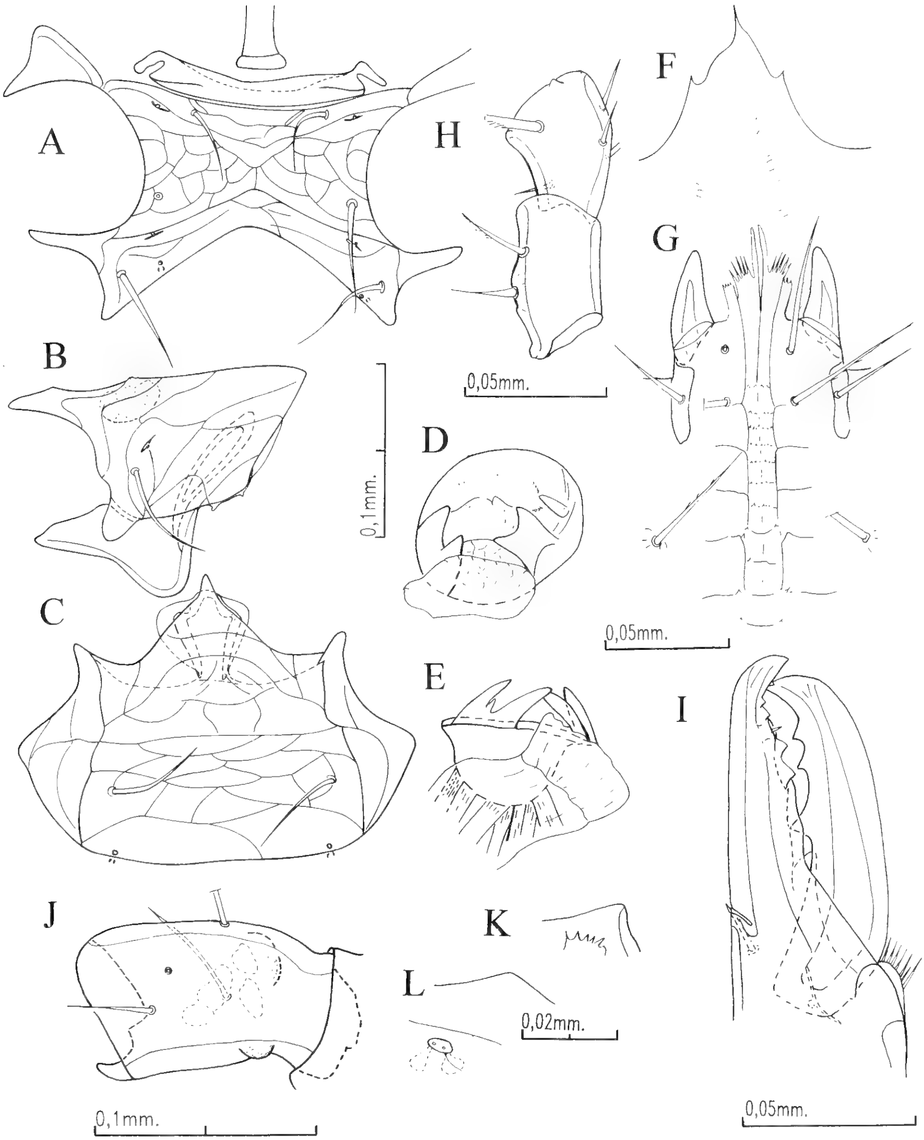


FIG.7

Holoparasitus cornutus sp. n. Female: A-presternal and sternal shields; B-paragynium; C-epigynium; D-endogynium (♀from Rumania); E-idem, (♀from Italy); F-tectum; G-hypognathal groove and corniculi; H-palptrochanter and palpfemur, antiaxial; I-chelicera, paraxial; J-trochanter IV, ventral; K-coxa II, denticulate ridge; L-gland gv2.

Female. Dimensions of idiosoma: 580 x 430 μm (L/W factor 1.35), specimen from Romania; 742-806 x 550-580 μm (L/W factor 1.34-1.41, N=5), specimens from Italy. Podonotal setae from 13 μm to 39 μm, j1 = 36-38 μm; opisthonotal setae shorter, about 13 μm.

Ventral side. Presternal shield smooth, ribbon-like, with two lateral excrescences, sternal shield with transverse ridge at level of pst2, some specimens with two lightly sclerotized indentations in front of setae st1 (Fig. 7 A). Sternal setae slender, 55-60 μm. Paragynial shield provided on its dorsal face with an elliptical thickening in front of coxa IV and on its inner ventral margin with one or two denticles; metagynial sclerite elongated, paragynial posterior protrusion elongated and rounded, paragynial lobe trapezoidal (Fig. 7 B). Epigynium heptagonal; its apex transparent, its subapical structure formed by a fine rounded margin and a sclerotized three-lobed thickening (Fig. 7 C). Endogynium: a rounded sack with two large, connected teeth on each side, covered by a scale flap ventrally, sometimes provided with denticles on inner walls; dorsally, its cuticle with many pores arranged in ca. 8 rows of muscle-prints (Fig. 7 D,E.). Gland pores behind each coxa IV located in a normal cuticle (Fig. 7 L). On opisthogaster 8 pairs of setae, their length from 40 μm (Jv1) to 24 μm (Jv5).

Gnathosoma. Tectum trispinate, lateral prongs tiny (Fig. 7 F). Hypognathal groove with 9-10 lines, anterior dentate, posterior bare; external posterior hypostomatic seta simple, other gnathosomal setae slightly pilose. Corniculi conical (Fig. 7 G).

Chelicera. Fixed digit with 3 minute denticles in front of pilus dentilis and behind it two teeth and a cuticular edge (Fig. 7 I).

Pedipalps. Trochanter with seta v1 simple and seta v2 slightly pilose. Femur with small protuberance near al seta (Fig. 7 H).

Legs. Coxa II with ridge bearing about 6 denticles (Fig. 7 K). Trochanter IV provided proximally with rounded protuberance on posterolateral face and with lamellar process, pointed in one or two spurs, dorsally or posterodorsally on distal margin of segment (Fig. 7 J). Measurements: tarsus I = 145 μm (specimen from Romania) and 164-173 μm (specimens from Italy); tarsus IV = 166 μm (Romania) and 189-196 μm (Italy).

Discussion. Juvara-Bals (1975) identified and described under the name of *H. apenninorum* (Berlese) specimens of *Holoparasitus* collected in the surroundings of Siena (Italy) and in Bucegi Mountain, Meridional Carpathians (Romania). She thought that the material belonged to *H. apenninorum* according to characteristics of male chelicera. In fact, Berlese (1906) had drawn two types of chelicera for *O. pollicipatus* var. *apenninorum*, as already discussed in the comments to the redescription of that species. Figure 16, tab. XIII by Berlese (1906) was a drawing of a specimen from Monte Senario which is the same as *H. cornutus*, the new species described above. The specimens of *H. cornutus* from Romania and Italy do not exhibit significant differences (Juvara-Bals, 1975). The male genital lamina is not serrated in specimens from Romania but instead it has only two central denticles. The number of teeth on the movable digit is 2 in Romanian versus 3 in Italian specimens and the shape of the tectum is slightly variable. *H. cornutus* is characterised especially by the lamellar process situated more or less dorsally on margin of trochanter IV in both sexes. Other characteristics

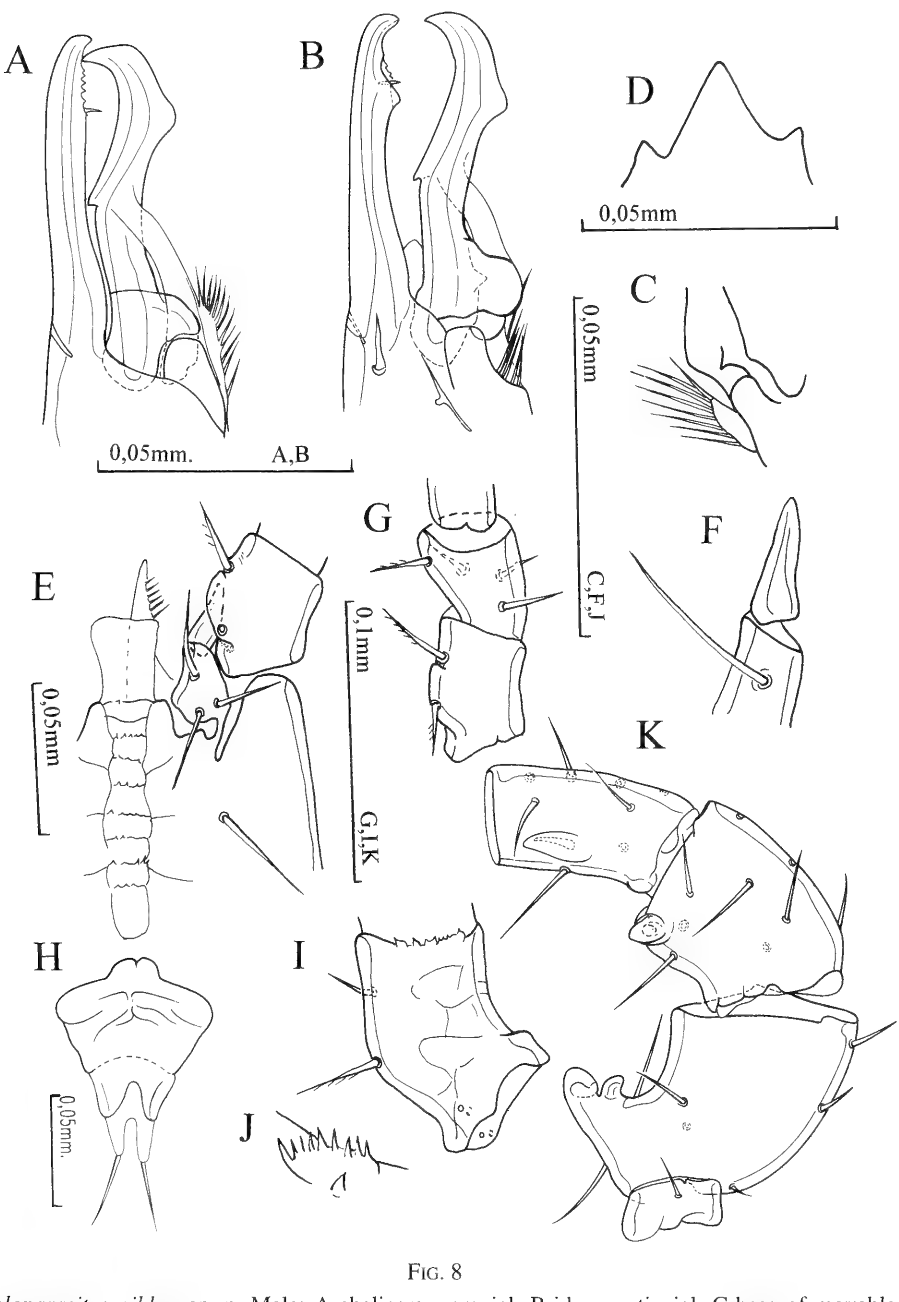


FIG. 8

Holoparasitus gibber sp. n. Male: A-chelicera, paraxial; B-idem, antiaxial; C-base of movable digit; D-tectum; E-gnathosoma and palptrochanter, ventral; F-corniculus; G-palptrochanter and palpfemur; H-genital lamina; I-coxa I, paraxial; J-coxa II, denticulate ridge; K-leg II, femur, genu and tibia.

such as the shape of the chelicera and armature of leg II in the male, as well as the particularities of the endo- and epigynium of the female distinguish this species from the other species belonging to the complex *O. pollicipatus* var. *apenninorum* sensu Berlese 1906. We also have to mention the species *H. hemisphaericus* (Vitzthum, 1923) described on the basis of a single female found in Austria. This species was considered by Juvara-Bals (1975) to be synonymous with *H. apenninorum* sensu Juvara-Bals, 1975. *H. cornutus* was compared with the type of *H. hemisphaericus* kindly sent to the senior author by Dr. L. Tiefenbacher (Munich, Germany). *H. hemisphaericus* is a valid species which differs from *H. cornutus* by the shape and size of the dorsal protuberance located distally on trochanter IV, by the absence of the proximal protuberance on trochanter IV, as well as by the paragynia, characterised by thickenings at paraxial margins but devoid of any thickening in front of coxa IV. Unfortunately, this species is known only on the basis of one female and on the single specimen available the characteristics of the epigynium and those of the endogynium cannot be properly observed.

Holoparasitus gibber sp. n. Figs 8, 9

The species is described from permanent slides of the Athias-Henriot collection. The length of the idiosoma cannot be measured because the specimens are crushed.

Type material: 1♂ holotype, 2♂♂, 3♀♀, 1 deutonymph, paratypes, Los Palacios (near Seville, Spain), sifting of flood litter, 22.02.1951, leg. H. Franz, and 4♂♂, 4♀♀, 1 deutonymph paratypes, surroundings of Carmona (near Seville, Spain), in the vicinity of Finca Alamaja, black soil from decayed plants, 22.02.1951, leg. H. Franz. All types in collection of Athias-Henriot deposited in MHNG.

Diagnosis. Male: excipulum absent; mobile digit of chelicera with 1 tooth, fixed digit with subapically located 6 denticles plus one (Fig. 8 A.B); hypostome extended between corniculi. Female: presternal plate with anterior margin serrated; endogynium circular in outline with two prolongations of posterior margin reaching anterior edge of endogynium, lateral sides of endogynial sack with 1-2 denticles (Fig. 9 D).

Description. Male. Idiosoma. Cuticle yellow-brownish, moderately sclerotized. Setae on holodorsal shield from 36 µm (j1) to 13-15 µm in opisthonotal region.

Ventral side. Sternal shield reticulated, without a particular pattern; length of sternal setae 24 µm (st2) to about 36 µm (st1, st4). Genital lamina with large central rounded process (Fig. 8 H). Opisthogaster with 8-9 pairs of setae, their lengths about 20 µm. Simple gland pore behind coxae IV.

Gnathosoma. Tectum with three prongs, the median much larger and broader than lateral ones (Fig. 8 D). Hypostome extended between corniculi; hypognathal groove provided with 9 rows of very fine denticles; hypostomatic and palpcoxal setae simple. Sclerotized cuticle with incisions behind hypostomatics; internal malae covered by a trapezoidal extension (Fig. 8 E). Corniculi slender and conical (Fig. 8 F).

Chelicera (Fig. 8 A-C). Fixed digit straight and narrow, its apex slightly curved; along its upper third, internal paraxial edge provided with 6 small denticles and antiaxial edge only with one big tooth; pilus dentilis located between these two edges. Movable digit with big tooth medially on internal margin and a characteristic rounded

hump on external (ventral) margin. Spermatotreme slender, ending distally at the level of tooth; the basal part of the digit with well sclerotized enlargement and a little denticle. Arthrodial membrane developed into brush-like process.

Pedipalps. Trochanter with protuberance located between slightly pilose setae v1 and thick and pilose v2; femur provided with small rounded protuberance, seta al slightly spatulate (Fig. 8 G).

Legs. Distal margin of coxa I dentate, coxa II with ridge bearing 7-8 denticles and an extra basal denticle (Fig. 8 I,J). Spurs on leg II as in figure 8 K: femoral apophysis short and thumb-like and axillary process trapezoidal; triangular spur located distally on genual margin; tibial apophysis elongated, situated medially on anterolateral face. Measurements: tarsus I = 159-169 μm; tarsus IV = 164-169 μm.

Female. Idiosoma. Colour yellow-brownish; setae on podonotal region from 46 μm (j1) to 26 μm; setae on opisthonotal region shorter, ca. 13 μm.

Ventral side. Presternal plate entire, ribbon-like, with the anterior margin serrated; lateral presternal platelets free. Sternal shield reticulated with a longitudinal granular strip medially (Fig. 9 A), length of sternal setae about 52 μm. Paragynial shields reticulated, metagynial sclerites oval (Fig. 9 B). Epigynium heptagonal, its anterior margin with triangular median apex and two lateral prominent spines; subapical epigynial structure formed by a weakly sclerotized rectangle and a hyaline structure stretching beyond epigynial margin in the form of two little wings (Fig. 9 C). Endogynium cup-shaped and circular in outline. Its posterior margin protrudes forward to form two long, sinuous prolongations with rounded tips reaching anterior edge of endogynial sack; lateral sides with 1-2 denticles (Fig. 9 D). Opisthogastric shield with 9 pairs of setae, their length from 42 μm (Zv1) to 24 μm (Jv5).

Gnathosoma. Tectum trispinate with long median prong and two tiny lateral prongs; dorsal face slightly granular (Fig. 9 E). Hypognathal groove with 9-10 rows of denticles, last four oligodentate; palpcoxal seta pilose, anterior hypostomatic seta slightly barbed, posterior setae simple (Fig. 9 F).

Pedipalps (Fig. 9 G). Border of trochanter thickened between pilose setae v1 and v2; distal margin of femur with small tubercle. Chelicera (Fig. 9 H) similar to that of *H. ellipticus*: fixed digit with five teeth and a long, thin cuticular ridge, movable digit with three teeth.

Legs. Structure and setation unremarkable. Denticulate ridge on coxa II as in the male (Fig. 9 I). Measurements: tarsus I = 156-163 μm; tarsus IV = 173-185 μm.

Discussion. Adults of *H. gibber* are similar to those of *H. mallorcae* and of *H. ellipticus*. All these species have in common: denticulation of the anterior margin of the female's presternal shield, the shape of the endogynium and the pattern of male's second leg armature; but they differ mainly in the shape of the male's chelicera and tectum as well as in the form of the female's epigynium. See comments following the description of *H. ellipticus*.

Holoparasitus ellipticus sp. n. Figs. 10, 11

Type material: 1♂ holotype, 11♂♂, 9♀♀ paratypes, Milazzo, Sicily, Italy from litter of olive trees, 24.03.1972; 1♂, 2♀♀ paratypes, Monti Peloritani, Sicily, from humus and litter in

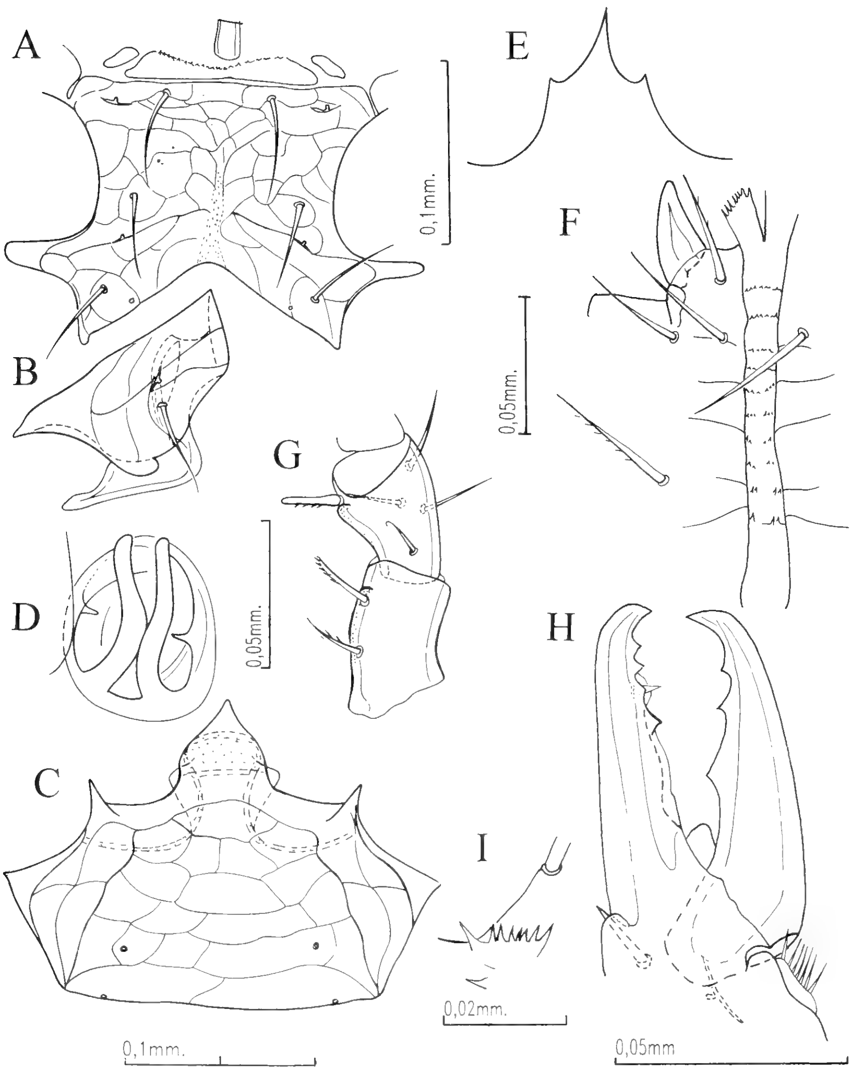


FIG. 9

Holoparasitus gibber sp. n. Female: A-presternal and sternal shields; B-paragynium; C-epigynium; D-endogynium; E-tectum; F-hypognathal groove and corniculus; G-palptrochanter and palpfemur; H-chelicera, paraxial; I-coxa II, denticulate ridge.

oak forest, 26.03.1972. The material was collected by the staff of the DEBS. The holotype and 3♂♂, 6♀♀ have been deposited in MHNG, whereas 9♂♂, 5♀♀ in ZMJU.

Diagnosis. Male: excipulum absent; mobile and fixed digits of chelicera with many denticles (Fig. 10 D,E); hypostome evidently extended between corniculi.

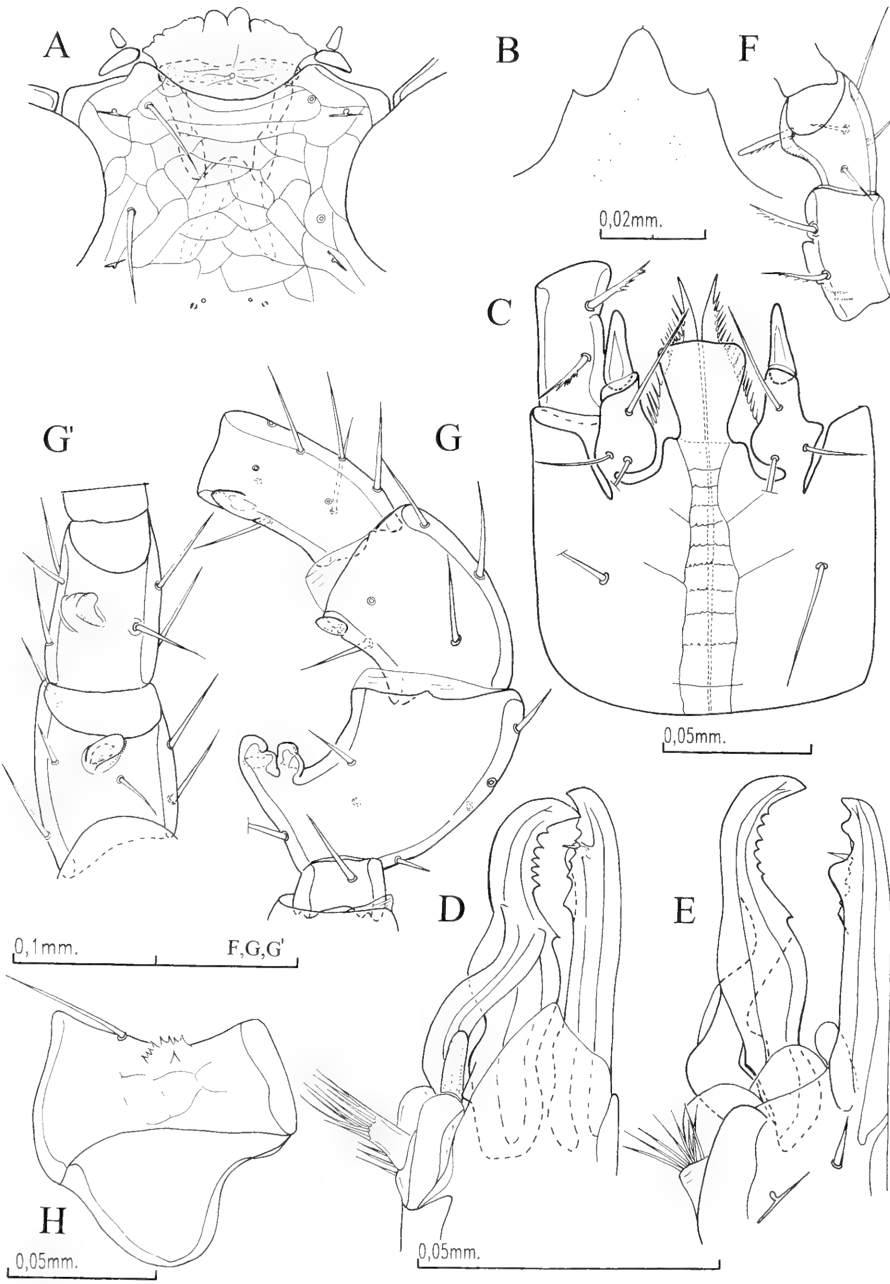


FIG. 10

Holoparasitus ellipticus sp. n. Male: A-genital lamina and sternogenital shields; B-tectum; C-gnathosoma and corniculi; D-chelicera, paraxial; E-idem, antiaxial; F-palptrochanter and palpfemur; G-G'-leg II, femur, genu and tibia antiaxial and ventral; H-coxa II, paraxial.

Female: presternal shield with anterior margin serrated; endogynium circular in outline; its posterior margin protrudes forward to form two prolongations ending beyond the anterior margin of endogynial sack; endogynial margin and walls with 3-7 denticles (Fig. 11 D).

Description. Male. Idiosoma markedly elongated, moderately sclerotized. Dimensions of idiosoma: 615-655 x 390-410 μm (L/W factor 1.57-1.64, N=10). Length of setae: podonotal region 15-20 μm, jl=39 μm and opisthonotal region 10-13 μm.

Ventral side. Genital opening located in a shallow concavity of sternal shield margin. Genital lamina divided into three lobes: central one bilobate, protruding forward more than lateral ones (Fig. 10 A). Sternogenital region with regular reticulation; length of sternal setae 39 μm. Cuticle around gland pores behind coxae IV not modified.

Gnathosoma. Tectum trispinate, with all lateral prongs terminated with minute spines; central prong rounded (Fig. 10 B). Hypostome with conspicuous broad extension located between slender corniculi. Hypognathal groove with 10 rows of denticles. Palpcoxal setae pilose, hypostomatic setae simple. Incisions in sclerotized cuticle behind hypostomatic setae (Fig.10 C).

Chelicera (Fig. 10 D,E). Fixed digit slender; its proximal 3/5 toothless, with parallel edges; distal part equipped with 4-5 small denticles paraxially, and pilus dentilis inserted in the vicinity of two more or less pronounced tubercles. Movable digit curved, bearing 5-7 denticles distally and large tooth medially; dorsal face of digit weakly sclerotized proximally. An elongated protuberance located paraxially at the base of spermatotreme. Arthrodial membrane with brush-like process developed paraxially, synarthrodial membrane rounded.

Pedipalps (Fig. 10 F). Paraxial border of trochanter slightly thickened, visible as a ridge, ending near seta v1; seta v1 thin and barbed along one edge, whereas seta v2 thick and richly pilose. Ventral surface of femur convex.

Legs. Legs I, III and IV unremarkable. Leg II spurred as follows (Fig. 10 G,G'): main spur on femur relatively short and rounded, axillary spur rounded and located close to main spur, both spurs end at the same level. Genu II with conical spur located distally and extending slightly beyond distal margin. Spur on tibia longer than that on genu, situated more paraxially and attached to tibia surface over a long distance. Ridge of 8 denticles and one solitary denticle on coxa II (Fig. 10 H). Measurements: tarsus I = 160-168 μm; tarsus IV = 173-184 μm.

Female. Idiosoma elongated but highly convex, cuticle moderately sclerotized, yellow to yellowish-brown. Dimensions of idiosoma: 690-770 x 465-540 μm (L/W factor 1.43-1.52, N=10). Podonotal setae: j1 = 45-46 μm, the others 20-39 μm; opisthonotal setae shorter, 10-14 μm.

Ventral side. Presternal plates entire, ribbon-like, with denticulate anterior margin; lateral presternal platelets free. Exopodal shields facing legs I with thickened anterior edge and connected to sternum via thin cuticle. Reticulation of sternum weakly pronounced, more visible in anterior region; posterior region with an axially running granulate strip (Fig. 11 A). Length of sternal setae from 52 μm to 59 μm.

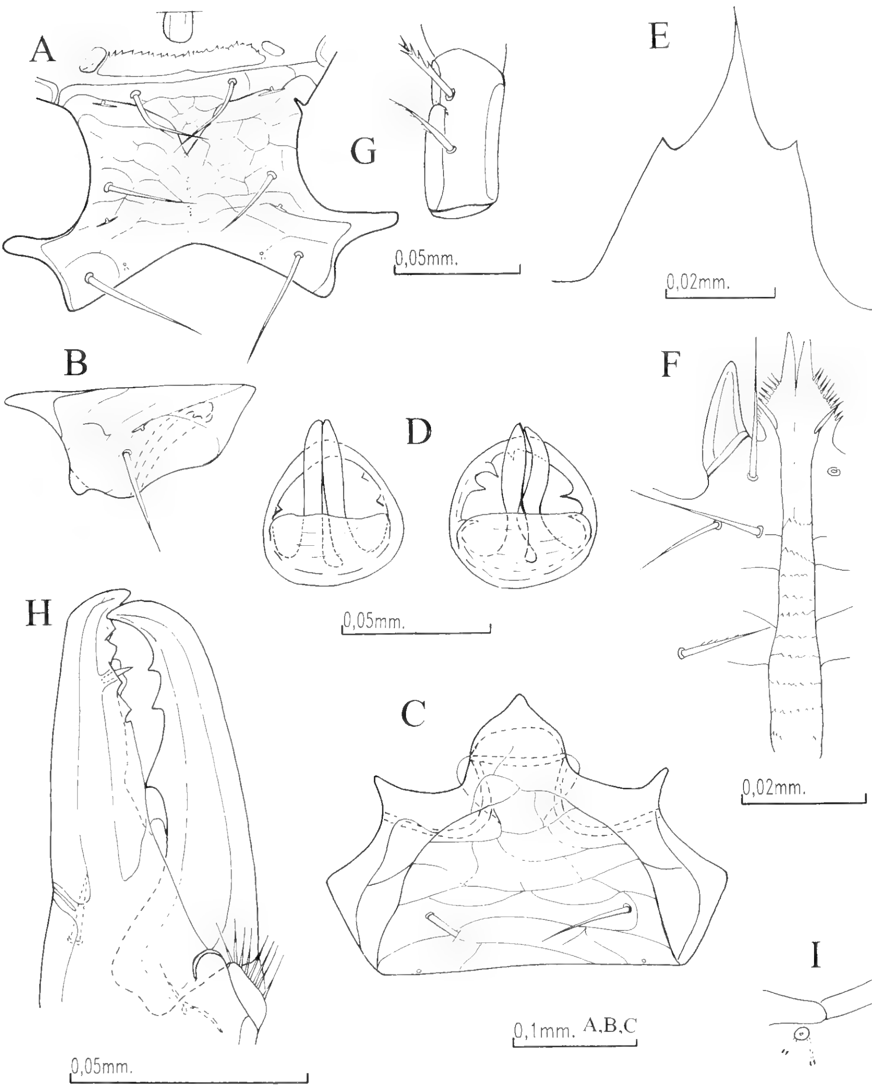


FIG. 11

Holoparasitus ellipticus sp. n. Female: A-presternal and sternal shields; B-paragynium; C-epigynium; D-endogynium; E-tectum; F-hypognathal groove and corniculus; G-palptrochanter; H- chelicera, paraxial; I-gland gv2.

Epigynium characterised by sharp lateral spines separated from central apex by deep concavities; lateral protrusions of subapical epigynial structure extending slightly beyond epigynium margin (Fig. 11 C). Paragynial shields with oval and slightly concave metagynial sclerites; thickenings in front of coxae IV absent. Paragynial

protrusions "locking" epigynial shield variable, ranging from ones with border paraxially angular to circular ones (Fig. 11 B). Cup-shaped endogynium circular; its posterior margin protrudes forward to form two slightly sinuous, tongue-like ribbons ending beyond anterior margin of endogynium; endogynial margin and walls armed with several (3-7) denticles, distributed more or less regularly. Endogynial opening covered with delicate lamina (Fig. 11 D). Opisthogaster with 8 pairs of setae, their length from 36 µm to 48 µm. Large, singular gland pores behind coxa IV surrounded by unmodified cuticle (Fig. 11 I).

Gnathosoma. Tectum trispinate, with long, attenuate median tine (Fig. 11 E). Hypognathal groove with 10 rows of denticles. Palpcoxal setae pilose, hypostomatic setae simple, corniculi conical (Fig. 11 F).

Chelicera (Fig. 11 H). Fixed digit with three teeth in front of pilus dentilis; sometimes central one smaller and located more paraxially. Pilus dentilis protected partially by truncated cuticular elevation; two teeth and a long, thin cuticular ridge located behind pilus dentilis. Movable digit with three teeth. Synarthrodial membrane rounded.

Pedipalps. Paraxial border of trochanter with a slightly thickened ridge, ending near pectinate seta v2, seta v1 pilose (Fig. 11 G). Anterolateral seta of femur spatulate and pectinate on one edge; genu with anterolateral setae simply spatulate.

Legs. Structure and setation unremarkable. Coxa II provided, on anterolateral face, with ridge of fine denticles plus one solitary denticle. Measurements: tarsus I = 164-168 µm; tarsus IV = 173-183 µm.

Discussion. H. ellipticus is very similar in morphology to *H. gibber*, as well as to four known species: *H. siculus* (Berlese, 1906), *H. mallorcae* Juvara-Bals, 1975, *H. maritimus* Hyatt, 1987 and *H. lawrencei*, Hyatt, 1987. These six species likely form a monophyletic species-group, which we name *mallorcae* group with characteristics listed below.

The males can be distinguished mainly due to: sternogenital shield without excipulum; hypostome (hypostomatic setae on distinct piece of cuticle, hypostome more or less evidently extended between corniculi); leg II (spur on femur relatively short).

The females share similar features for: presternal plates (anterior margin serrated, lateral platelets free); endogynium (cup-shaped, circular, with two prolongations from posterior margin); structure of genital shields (paragynia devoid of thickening in front of coxa IV, similar pattern of subapical epigynial structure); structure of chelicera (3 and 5 denticles on movable and fixed digits, respectively).

Differential diagnosis of the *Holoparasitus mallorcae* species-group.

Male:

1. corniculi indented, tectum with 3 prongs; mobile digit of chelicera with 4-6 denticles; fixed digit denticulated: *H. mallorcae* Juvara-Bals, 1975
2. corniculi indented, tectum with 1 prong; mobile digit of chelicera curved, enlarged in its upper third with 6 small denticles; fixed digit slender, truncate apically, with 2-3 denticles on inner margin: *H. siculus* (Berlese, 1905)

3. corniculi indented, tectum triangular; mobile digit of chelicera with 5 small denticles distally and 1 larger proximally; fixed digit slightly curved apically with 7-8 denticles : *H. maritimus* Hyatt, 1987
4. corniculi conical; mobile digit of chelicera with 6-7 denticles, its dorsal margin weakly sclerotized proximally, sclerotized microsclerite near basis of spermatotrema; fixed digit slender with one teeth and 7 denticles around pilus dentilis : *H. ellipticus* sp. n.
5. corniculi conical; mobile digit of chelicera with 1 tooth on internal edge and with one large protuberance on external edge of digit; fixed digit slender with 4 denticles and little tooth around pilus dentilis: *H. gibber* sp. n.
6. corniculi conical, mobile digit of chelicera with 1-2 teeth on internal edge;fixed digit edentate, finger-like: *H. lawrencei* Hyatt, 1987

Female:

1. apex of epigynium elongated: *H. siculus* (Berlese, 1905)
2. apex of epigynium normal; endogynium without teeth, endogynial margin prolongations arcuate: *H. maritimus* Hyatt, 1987
3. apex of epigynium normal; endogynium without teeth, endogynial margin prolongations straight: *H. mallorcae* Juvara-Bals, 1975
4. apex of epigynium normal; endogynium with two teeth, prolongations sinuous: *H. gibber* sp. n.
5. apex of epigynium normal; endogynium with several teeth, prolongations sinuous: *H. ellipticus* sp. n.
6. apex of epigynium enlarged with little tip medially; endogynium with many internal teeth, prolongations curved, usually with denticles or corrugations at the end: *H. lawrencei* Hyatt, 1987

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Three new species of *Geodia* Lamarck, 1815 (Porifera, Demospongiae) from the bathyal depths off Brazilian coast, Southwestern Atlantic

Carla Maria Menegola da SILVA[1] & Beatriz MOTHES[2]

[1] Universidade de São Paulo, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Av. Salvador França, 1427, 90690.000, Porto Alegre, RS, Brasil. E-mail: silva@portoweb.com.br

[2] Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Caixa Postal 1188, 90001-970, Porto Alegre, RS, Brasil. E-mail: bmothes@portoweb.com.br

Three new species of *Geodia* Lamarck, 1815 (Porifera, Demospongiae) from the bathyal depths off Brazilian coast, Southwestern Atlantic. - This work comprises a taxonomic study of tetractinellid sponges from a poorly known region in the southwestern Atlantic, off the Rio Grande do Sul State coast, Brazil (31°05'–32°00'S/49°31'-50°00'W). Samples were collected by R/V "Atlântico Sul" of Fundação Universidade do Rio Grande in a continental slope survey ("Projeto Talude") and R/V "Prof. W. Besnard", of Instituto Oceanográfico da Universidade de São Paulo/Group for the Development of the Fisheries Industry, in Rio Grande do Sul I Cruise. Three new species are described: *Geodia australis*, *G. splendida* and *G. riograndensis*.

Key-words: Porifera - *Geodia* - Rio Grande do Sul - Brazil - taxonomy - continental slope.

INTRODUCTION

Six species of *Geodia* are registered for the Brazilian coast: *Geodia gibberosa* Lamarck, 1815 (Laubenfels, 1956), *Geodia neptuni* (Sollas, 1886, 1888 as *Synops neptuni*; Mothes, 1996), *Geodia tylastra* Boury-Esnault, 1973 (Boury-Esnault, 1973), *Geodia papyracea* Hechtel, 1976 (Hechtel, 1976), *Geodia corticostylifera* Hajdu *et al.*, 1992 (Hajdu *et al.*, 1992) and Geodia glariosa (Sollas, 1886, 1888 and Volkmer-Ribeiro & Mothes-de-Moraes, 1975 as *Cydonium glariosus*).

The present paper describes three new species dredged off Rio Grande do Sul State coast (31°05'-32°00'S/49°31'-50°00'W) (fig. 1), in the slope region (207 to 520 m depth), during oceanographic expeditions carried out by R/V "Atlântico Sul", of

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Fundação Universidade do Rio Grande, Projeto Talude; and by R/V "Prof. W. Besnard", of Instituto Oceanográfico, Universidade de São Paulo, in agreement with Group for the Development of the Fisheries Industry, in Rio Grande do Sul I Cruise.

The influence of the Subtropical Convergence, with marked seasonal latitudinal displacement, characterizes the southern/southeastern Brazilian continental shelf and slope regions (23°S-34°S) as a biogeographic transition zone (Mothes, 1996; Sharp, 1988) between the large neritic areas of Patagonia and tropical Brazil. The composition and abundance of species, the pelagic structure, the spatial distribution of communities and their trophic interactions, as well as biological production are largely controlled by the seasonal dominance of distinct water masses over shelf and slope. The studied material was collected in the summer period (october to april), when the influence of Tropical Waters is greatest, though waters of subantarctic origin may also rise during the summer along the southernmost shelf break regions.

The paratypes of *Geodia australis* sp. n. were collected between Sarita and Rio Grande localities, 101 Km off Rio Grande do Sul coast, with temperature of 14,50°C and salinity 35,76‰. The holotype of this species was collected between Mostardas and Solidão localities, 58 Km off Rio Grande do Sul coast. Temperature and salinity data for this sample are not known, as well as for the type-specimens of *Geodia splendida* sp. n. and *G. riograndensis* sp. n.

MATERIAL AND METHODS

The samples are deposited in the Porifera Collection of Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul (MCN/ FZB).

Abbreviations used are:

BMNH Natural History Museum, London
MCN/FZB Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil
MHNG Muséum d'histoire naturelle Genève, Switzerland
UFRJ Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil
ZMA Zoölogisch Museum Amsterdam, Netherlands

The methodology used to prepare thick sections and dissociated spicules slides follow Mothes-de-Moraes (1978). Electron micrographs were taken at MCN/FZB with a Jeol 5200 equipment, with an accelerating voltage of 25 kV and magnifications varying from 1,500 to 10,000 times. Spicule measurements refer to minimum, *mean*, and maximum sizes in micrometers (µm) and were obtained by taking 50 measures of each type of spicule/specimen (unless stated otherwise).

DESCRIPTIONS

Order Astrophorida
Geodiidae Gray, 1867
Geodia Lamarck, 1815

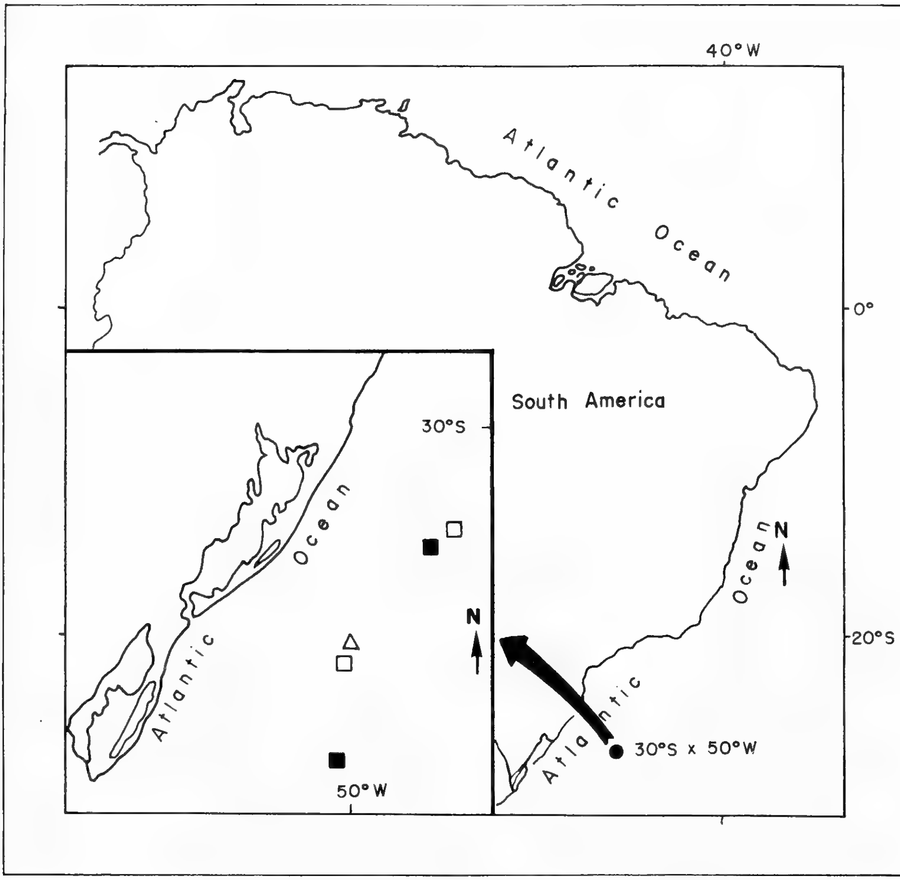


FIG. 1

Map of South American Coast with the Rio Grande do Sul State Coast in detail, showing the geographic distribution of *Geodia australis* sp. n. (■), *G. splendida* sp. n. (Δ) and *G. riograndensis* sp. n. (□).

Type-species: *Geodia gibberosa* Lamarck, 1815

Definition: Geodiidae with afferent and efferent aquiferous system independently, with well developed and large subectosomal spaces. Megascleres triaenes. Microscleres sterrasters and euasters of different types. Sterrasters varying from flattened or globose young forms, smooth with many spherical spaces or provided of conical and short rays, with blunt or strongiliform ends sometimes presenting small distal holes, to globose forms provided of star or rosette like microspinature at the distal end (adapted from Desqueyroux-Faúndez & Van Soest, 1997).

Geodia australis sp. n. Figs 1, 2, 5, 7, 11-26

Material: Holotype MCN 330, R/V "Prof. W. Besnard", off Rio Grande do Sul State coast, St. 458 (33°29'S/50°44'W), 9/XII/1968, 207 m, rocky substrate; Paratype MHNG-INVE

26564 (schizoparatype-slides deposited in the MCN 331), same data of the holotype; Paratype ZMA POR13418 (schizoparatype-slides deposited in the MCN 332), R/V "Prof. W. Besnard", off Rio Grande do Sul State coast, St. 444 (31°31'00"S/49°47'00"W), 6/XII/1968, 284 m, rocky substrate.

Description: Spherical sponge (fig. 2) (diameter 3.8 cm x 3.1 cm, height 2.8 cm). Hispid surface, with slight brushes of oxeas (fig. 7); small openings are observed in some points of the surface, which could not be differentiated in ostia or oscula. Colour in spirit grayish-white; compressible consistency. The sponges are associated with polychaets and corals.

Skeleton: Ectosomal (fig. 5): cortex (0.5 mm thick) with spherasters of variable sizes, over several layers of sterrasters ended at the cladome-layer of the dichotriaenes, plagiotriaenes and protriaenes; scattered small oxeas, strewn at random, are also observed.

Choanosomal (fig. 5): formed by dichotriaenes, plagiotriaenes, protriaenes and large oxeas, the last ones preferentially arranged in radial bundles, forming a right angle with the cortex. Besides the triaenes and oxeas, sterrasters, spherasters and oxyasters are abundantly spread.

Spicules: Oxeas I (fig. 12): fusiform, straight or slightly curved, with pointed or blunt ends; some with mucronate ends; length 1403-*2285.7*-3818/24-*31.0*-40 µm.

Oxeas II (fig. 13): fusiform, with gradually pointed ends; length 181-*275.1*-418/3.2-*4.8*-6.9 µm.

Dichotriaenes (fig. 11): conical rhabdom, with gradually pointed or strongyloid end. Cladi are first curved upwards and then slightly downwards; rhabdome 1012-*2246.0*-3565/33-*61.0*-86 µm; cladome 333-*553.8*-703 µm, protocladi 161-*192.1*-238/29-*38.7*-48 µm; deuterocladi 76-*107.2*-143 µm.

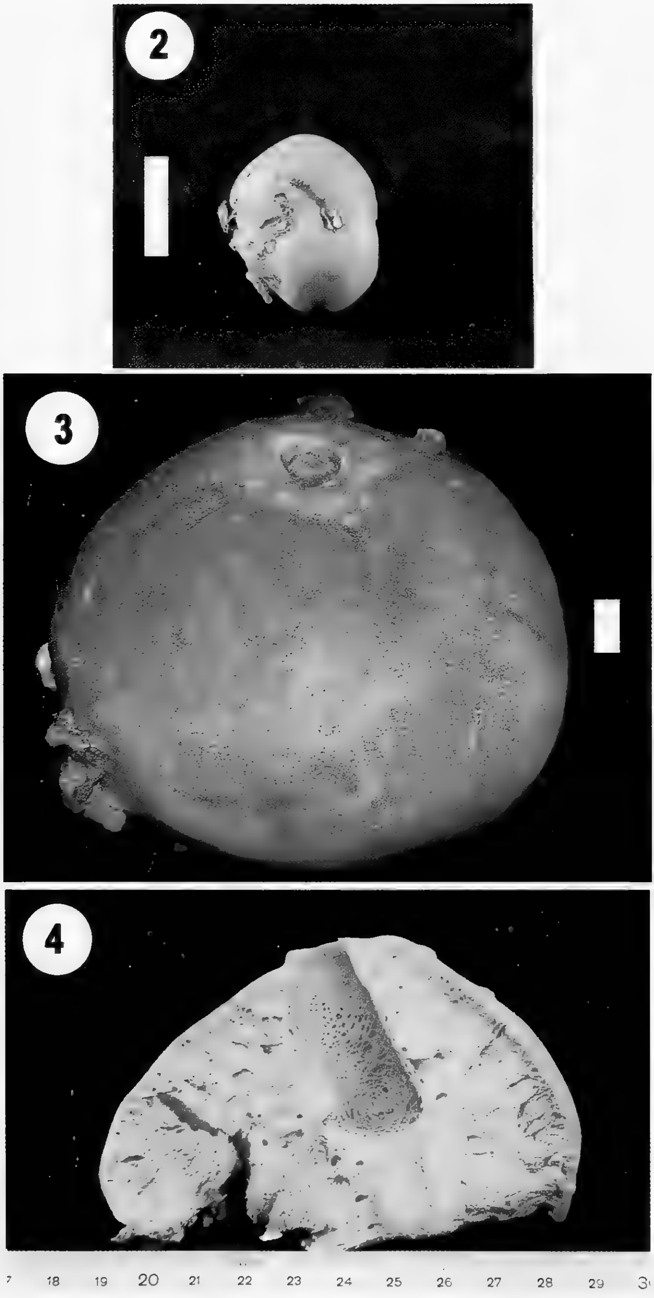
Protriaenes (fig. 17): conical, thin rhabdome, with gradually pointed or blunt end; cladi with thin ends, sometimes provided with a constriction; rhabdome 1334-*3143.9*-5865/4.6-*10.4*-23 µm; cladome 86-*154.2*-276 µm, cladi 67-*156.4*-276/4.6-*8.2*-14 µm.

Plagiotriaenes (fig. 16): rare (N=5), rhabdome conical, straight and thin, with gradually pointed end; cladi with thin ends; rhabdome 828-1909/19-28.5 µm; cladome 105-219 µm; cladi 51-131/11.5-18.4 µm.

Anatriaenes (fig. 14): rhabdome conical and thin, with pointed or strongyloid end; cladi with pointed ends, sometimes marked by a constriction; rhabdome 1150-*3450.0*-6140/4.8-*14.2*-24 µm; cladome 67-*130.9*-190 µm, cladi 48-*110.6*-181 µm. Some rares (N=5), slender and smaller anatriaenes (fig. 15) can be observed: rhabdome 323-423/3.4-4.6 µm; cladome 6.9-9.2 µm; cladi 2.3-4.6/1.1-1.8 µm.

Sterrasters (figs. 18-20): oval or more rarely spherical, the young scleres with microspined surface in the shape of pointed cones and in the shape of a star in adult scleres; diameter 266-*314.8*-352/190-*253.6*-295 µm.

Spherasters (fig. 21): spherical with well delimited center, variable size and short conical spines with blunt ends; in the choanosome, the largest spherasters can be taken for young sterrasters, differing by the shape of the microspines; diameter 20-*26.3*-32 µm.



FIGS 2-4

Habit: 2, *Geodia australis* sp. n.; 3, *G. splendida* sp. n.; 3, *G. riograndensis* sp. n.-inner view in transversal section. Scale = 2 cm.

Oxyasters I (fig. 22): small and smooth center; 4 to 7 long, conical and microspined rays; total diameter 35-*43.2*-52 µm, diameter of the centrum 2.3-*4.3*-6.9 µm, rays 9-*16.9*-25/1.5-*2.3*-3.5 µm.

Oxyasters II (fig. 23): small and smooth center: 8 to 11 long, conical and microspined rays; total diameter 16-*23.7*-32 µm, diameter of the centrum 2.3-*4.2*-5.8 µm, rays 6.9-*10.0*-13.8/2.3 µm.

Spheroxyasters (fig. 26): discrete center; 15 to 22 short , conical and scarcely microspined rays; total diameter 14-*16.1*-20 µm, diameter of the centrum 4.6-*5.7*-6.9 µm, rays 3.4-*4.5*-5.7/1.8-*2.2*-2.8 µm.

Spherostrongylasters: clear and smooth; 7 to 14 short, blunt rays, with conical microspines; total diameter 4.6-*7.0*-9.2 µm, diameter of the centrum 2.3-*2.8*-3.4 µm, rays 1.8-*2.3*-2.8/≤1.0 µm.

Etymology: The specific name refers to the type-locality, off Brazil's southern region [Latin word *australis* = southern; south].

Remarks: The samples utilized in this description were identified by Mothes-de-Moraes (1978) as *Geodia eosaster* (Sollas, 1886).

Hajdu *et al.* (1992) advanced the idea that *G. eosaster sensu* Mothes-de-Moraes (1978) could be a new species due to its widely disjunct distribution when compared to the original record of *G. eosaster* from Australia (Sollas, 1886; 1888). Our reexamination of Mothes-de-Moraes (1978) specimens, when compared with the syntype of *G. eosaster* [BMNH 1889.1.1.87], revealed several spicular micrometric distinctions and the SEM analysis confirmed the presence of adittional categories of megascleres and microscleres. We thus described them as *Geodia australis* sp. n.

Both species share the presence of dichotriaenes, protriaenes, spherasters and strongylasters, but they can be distinguished by the occurrence of rare plagiotriaenes, oval shaped sterrasters, and of a second type of oxyaster in the new species.

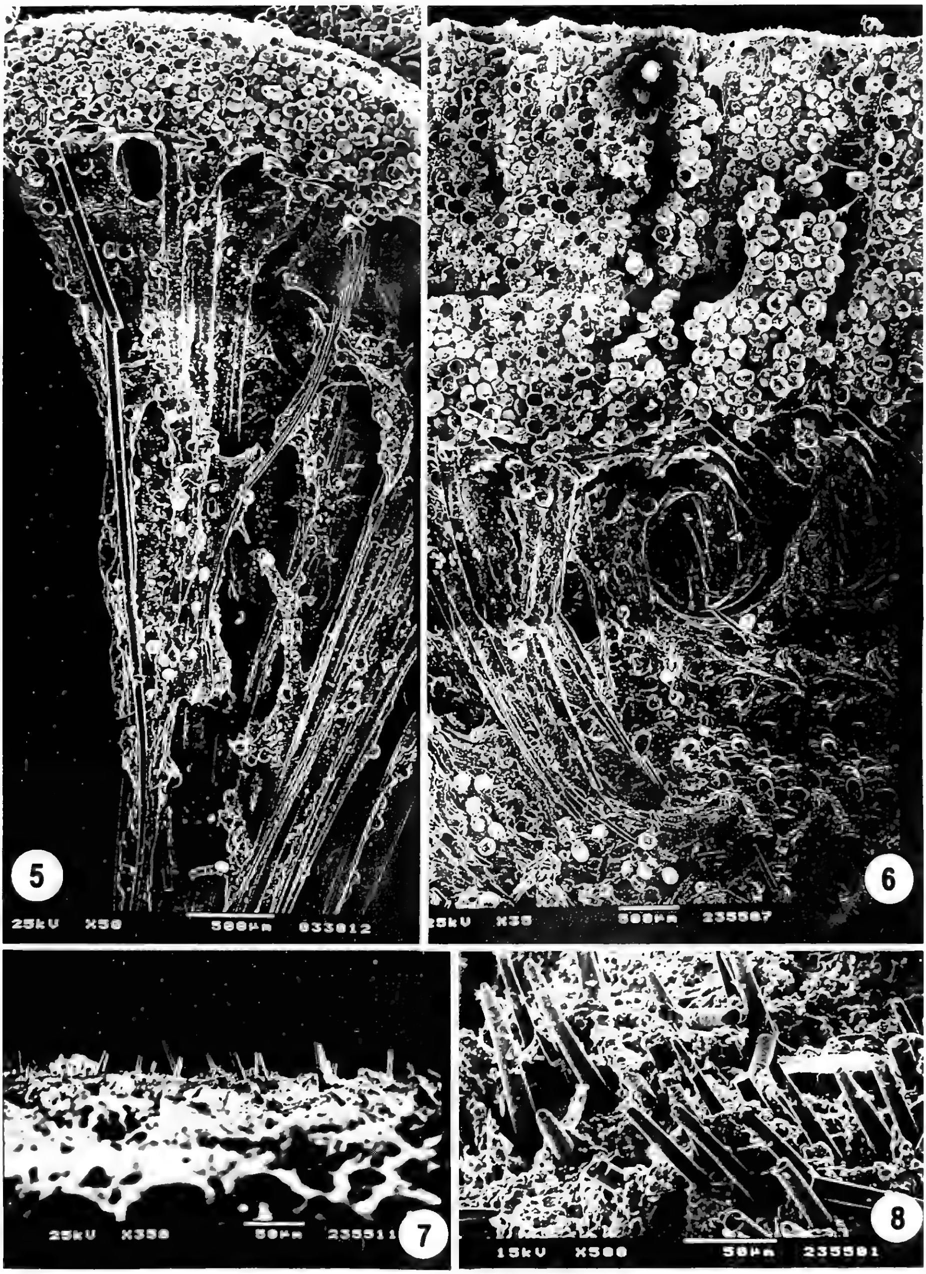
From the Tropical western Atlantic records of *Geodia*, the new species appears closest to *G. spherastrea* Lévi, 1964, from deep-waters off Puerto Rico, at 2840 m depth. Both species share the presence of dichotriaenes, protriaenes, anatriaenes, spherasters and strongylasters, but can be distinguished by the occurrence of rare plagiotriaenes, oxyasters and oval shaped sterrasters in the new species.

The "somal" spherasters of *Geodia eosaster* (Sollas, 1886) and the chiasters [=strongylasters *sensu* Boury-Esnault & Rützler, 1997] of *G. spherastrea* (Lévi, 1964), correspond to the spherostrongylasters here described for *G. australis* sp. n. The term was coined for cases where the width of the aster's centrum exceeds 1/3 of the microscleres total diameter.

Geodia splendida sp. n. Figs 1, 3, 6, 8, 27-39

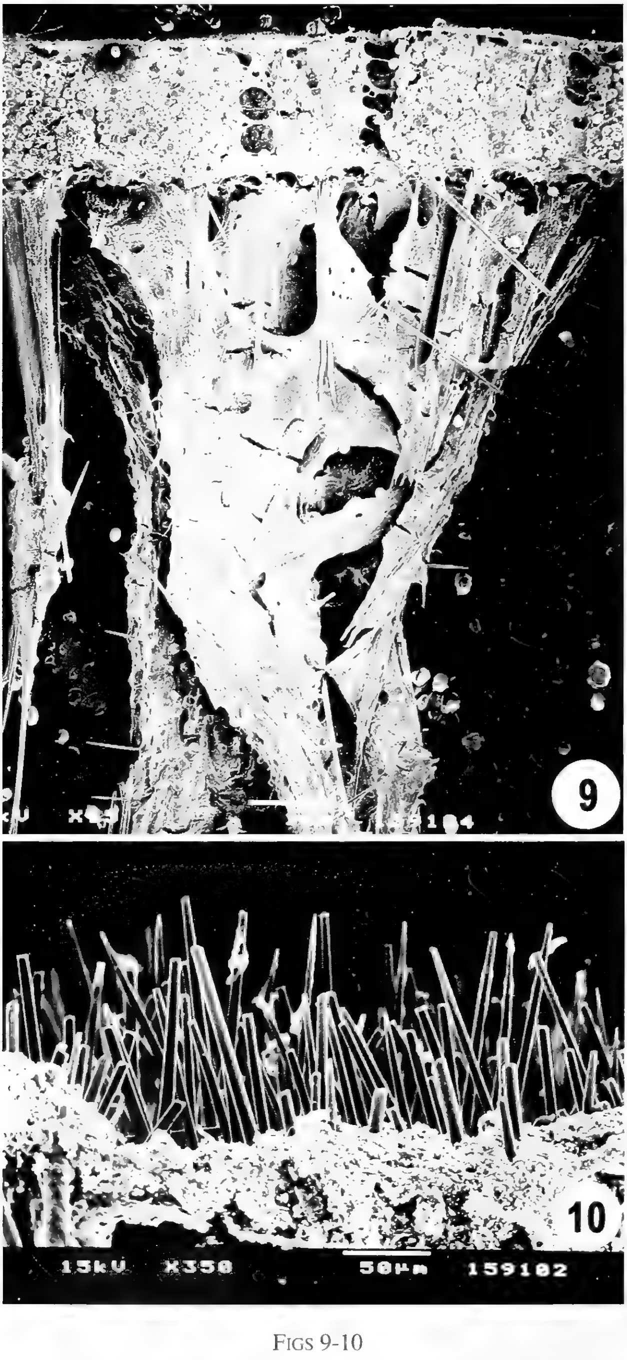
Material: Holotype MCN 2355 (schizoholotype MHNG-INVE 26565), R/V "Atlântico Sul", off Rio Grande do Sul State coast, St. 10 (32°00'S/50°00'W), 10-X-1991, 520 m, rocky bottom.

Description: Globose sponge (fig. 3), diameter 27 cm, height 24 cm. Surface smooth to the touch; single oscule, apical, central, elypsoidal, diameter 3.5/3 cm, at the



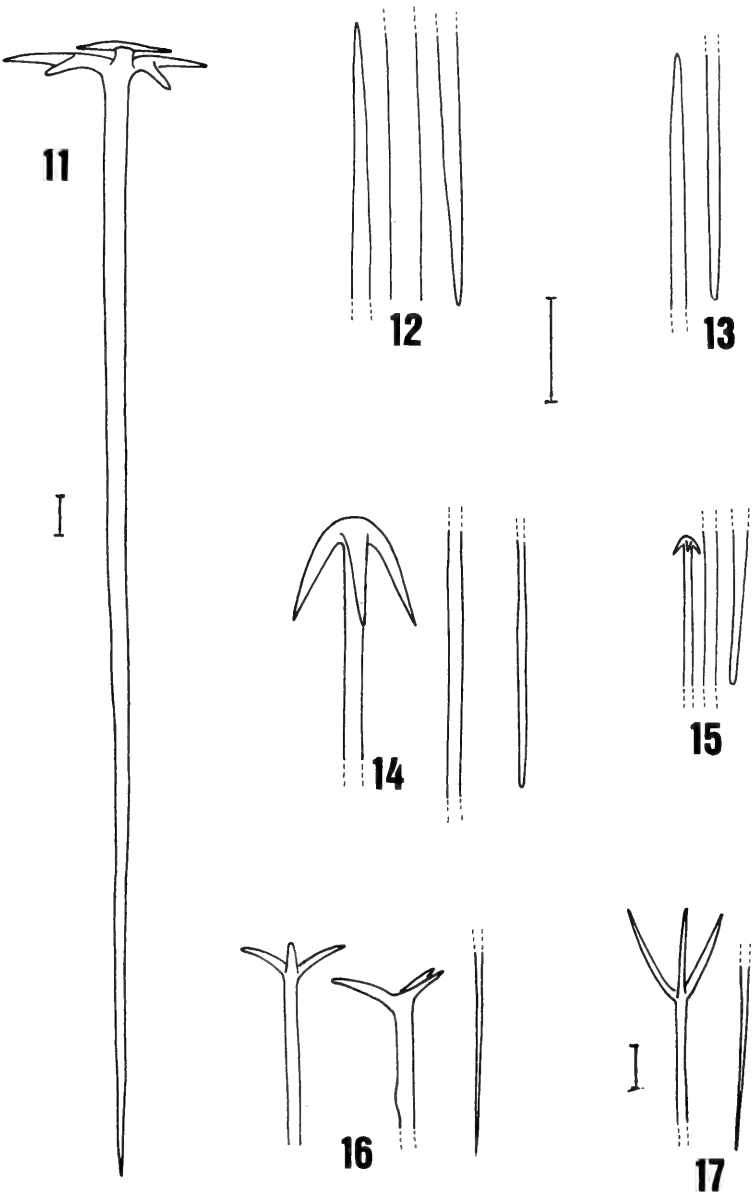
FIGS 5-8

Skeleton: 5, 6.Skeletal arrangement. 5, *Geodia australis* sp. n.; 6. *G. splendida* sp. n.; 7, 8. Sponge surface : 7, *G. australis* sp. n.; 8, *G. splendida* sp. n.



FIGS 9-10

Geodia riograndensis sp. n.: 9, skeletal architecture; 10, oxeas protracting at the sponge surface.



FIGS 11-17

Megascleres of *Geodia australis* sp. n.: 11, dichotriaene; 12, oxeas I; 13, oxea II; 14, anatriaene; 15. smaller anatriaene; 16, plagiotriaene; 17, protriaene. Scales = 100 µm.

terminal part of a cylindrical channel (length 12 cm), in the inner lateral walls of which the exhalant channel openings can be observed; pores not visible. Preserved material of violet colour and hard consistency.

Skeleton: Ectosomal (fig. 6): cortex made up of several overlaping layers of sterrasters (0.6-0.7 cm) and the discrete protraction of robust oxeas and some rare styloid forms (fig. 8); the cladomes of the orthotriaenes are placed parallel to the sponge surface just below the cortex.

Choanosomal (fig. 6): formed by the rhabdoms of the orthotriaenes, perpendicular to the surface and, among them, long oxeas, randomly distributed and rare sterrasters.

Spicules: Oxeas I (fig. 27): straight or slightly bent, robust, with ends blunt or gradually pointed, length 2254-*2681.0*-3151/ width 28-*44.2*-62 µm.

Oxeas II (fig. 30): straight or slightly curved, with gradually pointed or mucronate ends; some thinner scleres have blunt ends. Length 228-*432.7*-684 µm, width 5.7-*10.7*-19 µm.

Orthotriaenes (figs 28, 29): straigth; cladi straight or bent downward at their distal portion, with blunt or gradually sharpening ends; length 3266-*3689*.0-4094 µm, width 104-*111.6*-120 µm, cladome diameter 920-*1165.7*-1495 µm.; cladi length 437-*589.8*-759 µm, cladi width at the base 85-*100.8*-113 µm.

Sterrasters (figs 31-36): spherical or ellipsoidal, with conspicuous hilum, microspined at the outer portion (figs 34, 35); surface with rounded holes (figs. 31, 32) or conical rays (fig. 33) in young forms; or provided with regular microspinature in star shape in adult scleres (figs 34-36); diameter 95-148.2-171/86-*119.7*-152 µm.

Oxyasters I (fig. 37): 4 to 8 microspined rays all along their length; total diameter 78-*100.1*-131 µm, center 6.9-*9.2*-13.8 µm, rays 35-*46.9*-62/2.8-*4.7*-6.9 µm.

Oxyasters II (fig. 38): 4 to 9 rays provided with conical microspines all along their length, total diameter 12-*17.9*-23 µm, center 1.6-*2.3*-3.4 µm, rays length 4.6-*7.9*-11.5 µm, rays width < 1 µm.

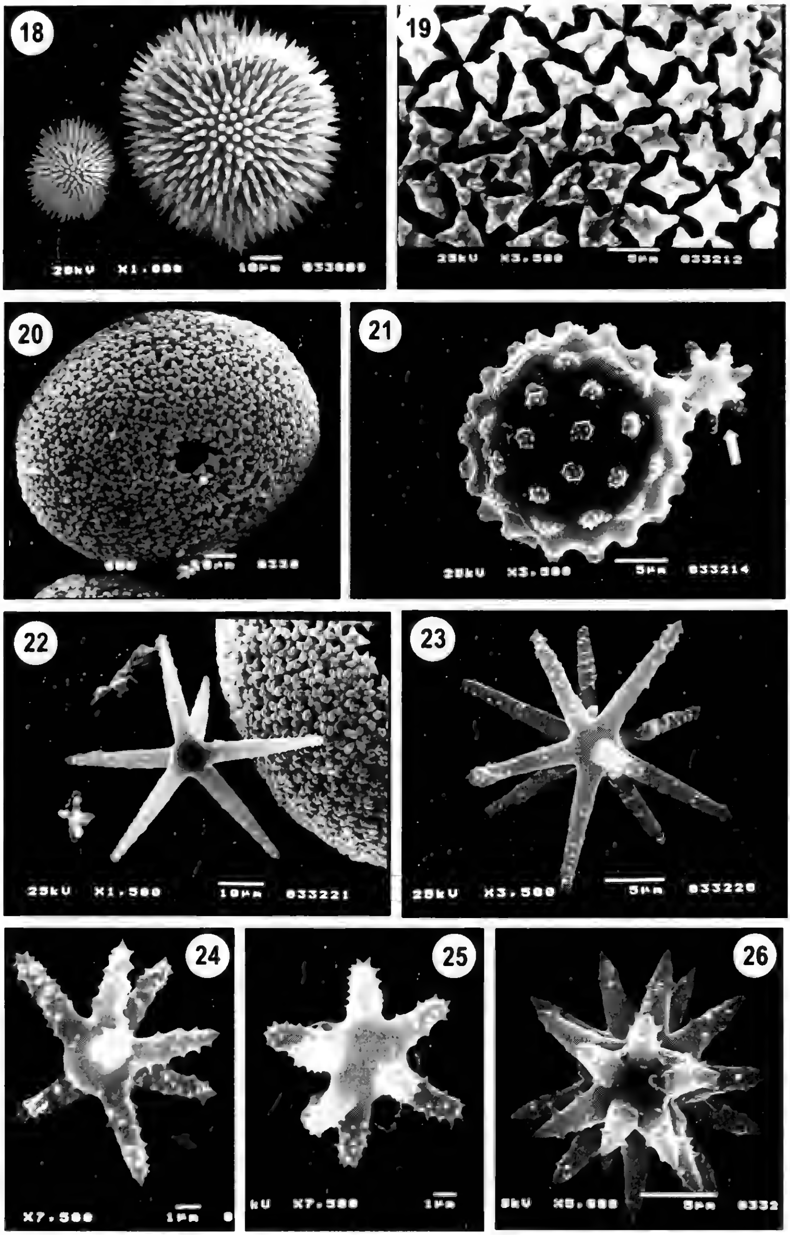
Spherostrongylasters (fig. 39): 5 to 11 microspined rays all along their length, with blunt ends, diameter 5.5-*7.4*-9.9 µm, rays 1.1-*1.5*-2.2/<1.0-1.5 µm.

Etymology: The specific name refers to the beauty and large size of the specimen. [Latin word *splendidus* = magnific]

Remarks: Geodia splendida sp. n. is close to *Geodia corticostylifera* Hajdu *et al.*, 1992 [Holotype UFRJ POR 3098 and Paratype UFRJ POR 3714, examined] by the shared presence of oxeas, orthotriaenes and oxyasters. They both differ nevertheless by the presence of an additional category of styles instead of oxeas in *G. corticostylifera* and of microscleres of the spheroxyaster and strongylospheraster types in *G. splendida* sp. n.

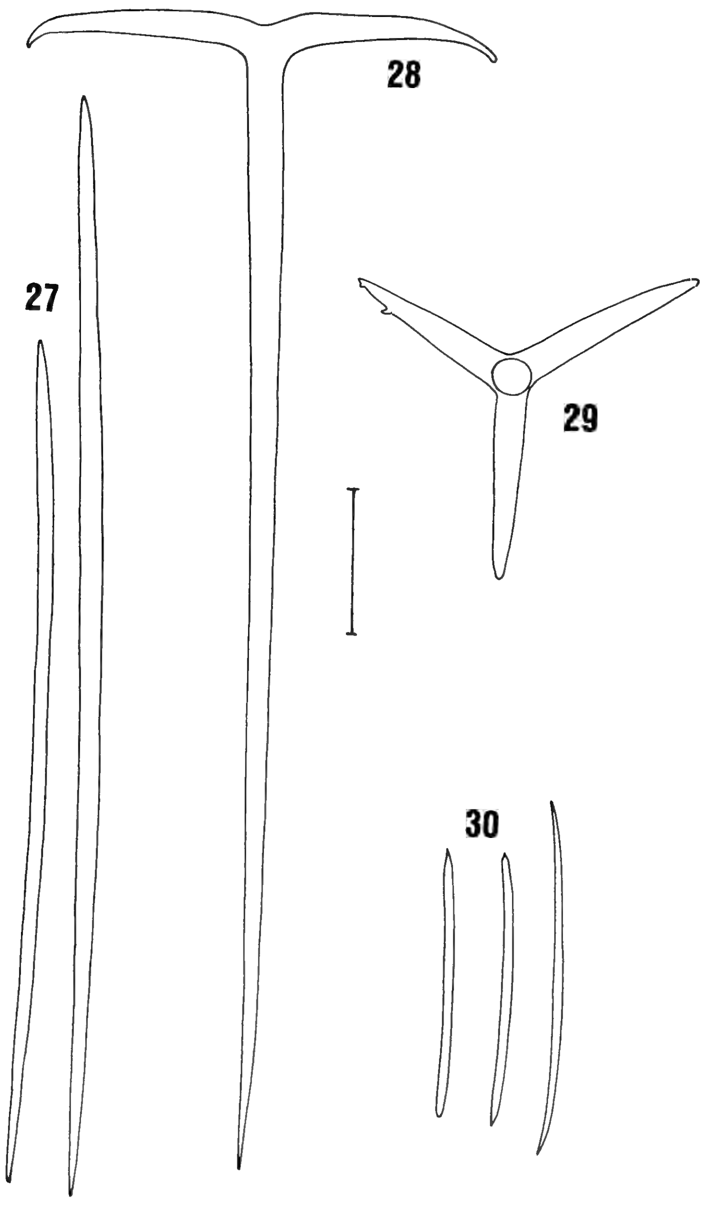
Geodia riograndensis sp. n. Figs 1, 4, 9, 10, 40-58

Material: Holotype MCN 1591 (schizoholotype MHNG-INVE 26566),"R/V Atlântico Sul", off Rio Grande do Sul State coast, St. 2-26 (31°05'S/49°31'W), 15-II-1987, 300 m, rocky substrate; Paratype MCN 3452, R/V . "Atlântico Sul", off Rio Grande do Sul State coast, St. 1-5 (32°24'55"S/50°14'85"W), 30/IV/1986, 200 m, rocky substrate.



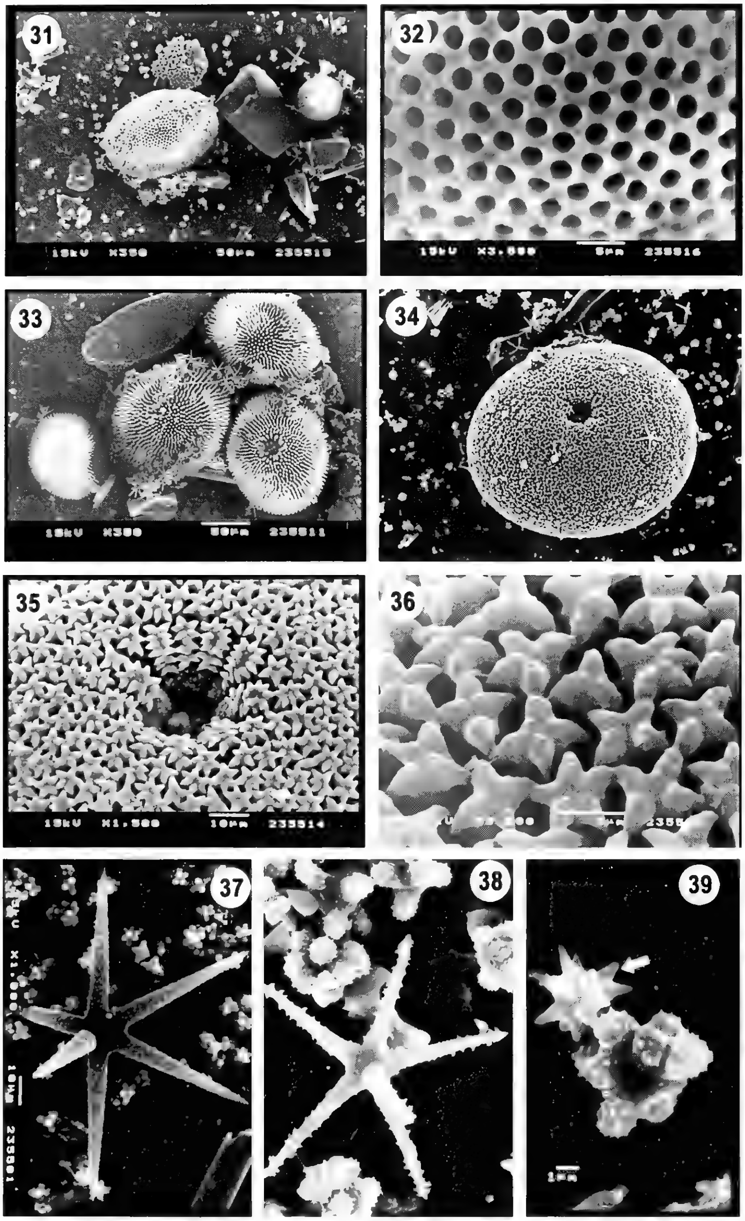
FIGS 18-26

Microscleres of *Geodia australis* sp. n.: 18, young sterraster; 19, adult sterraster surface; 20, adult sterraster with hilum; 21, spheraster and spherostrongylaster (arrow); 22, oxyaster I; 23, oxyaster II; 24, spherostrongylaster with conical tips; 25, spherostrongylaster; 26, spheroxyaster.



FIGS 27-30

Megascleres of *Geodia splendida* sp. n.: 27, oxea I; 28, orthotriaene; 29, orthotriaene cladome in apical view; 30, oxeas II. Scale = 500 µm.



FIGS 31-39

Microscleres of *Geodia splendida* sp. n.: 31, 33 sterraster developmental stage; 32, sterraster developmental stage surface; 34, adult sterraster; 35, sterraster surface with hilum; 36, adult sterraster showing microspinature details; 37, oxyaster I; 38, oxyaster II; 39, spherostrongylaster developmental stage (arrow) and grown spherostrongylaster.

Description: Subglobose fragment (fig. 4), diameter 10.6 cm, height 7.5 cm. Hispid surface, with slight brushes of oxeas (0.2-0.5 mm) (fig. 10); central oscule (diameter 11 mm), raising above the surface (3 mm), at the terminal part of a cylindric channel (length 44 mm), in the inner lateral wall of which the opening of the exhallant channels can be observed; pores were not observed. Preserved material with beige colour and firm consistency.

Skeleton: Ectosomal (fig. 9): Cortex made up by large quantities of sterrasters in regular overlapping layers, throughout which, small and thin oxeas are found and, more rarely, very long oxeas with filiform ends, both projecting slightly above the sponge surface. In the subcortical area orthotriaenes and additional categories of triaenes are distributed slant or perpendicular to the surface, the latter being hardly observed.

Choanosomal (fig. 9): formed by tracts of oxeas perpendicular to the surface and rare sterrasters of random distribution.

Spicules: Oxeas I (fig. 42): thin, sinuous, with gradually pointed ends, length 2415-*5720.5*-8464 µm, width: 12-*17.5*-23 µm.

Oxeas II (fig. 43): robust, straight or slightly curved, with blunt or mucronate ends. Some scleres thinner, with one of the ends presenting lateral conical expansions, from which one of the sclere sides becomes gradually thinner, length 1610-*2082.0*-2726 µm, width 21-*35.2*-46 µm.

Oxeas III (fig. 44): straight or slightly curved, with gradually pointed ends, length 247-*486.6*-741 µm, width 5.7-*8.9*-11.4 µm.

Orthotriaenes (figs 40, 41): straight rhabd with end conical or sharpening gradually; straight or downwards cladi with conical or strongyliform distal ends, sometimes bi- or trifurcate, length 1725-*2819.8*-3675 µm, width 44-*66.5*-92 µm, cladome diameter 575-*775.3*-989 µm, cladi length 253-*365.4*-437 µm, cladi thickness at the base 32-*55.0*-69 µm.

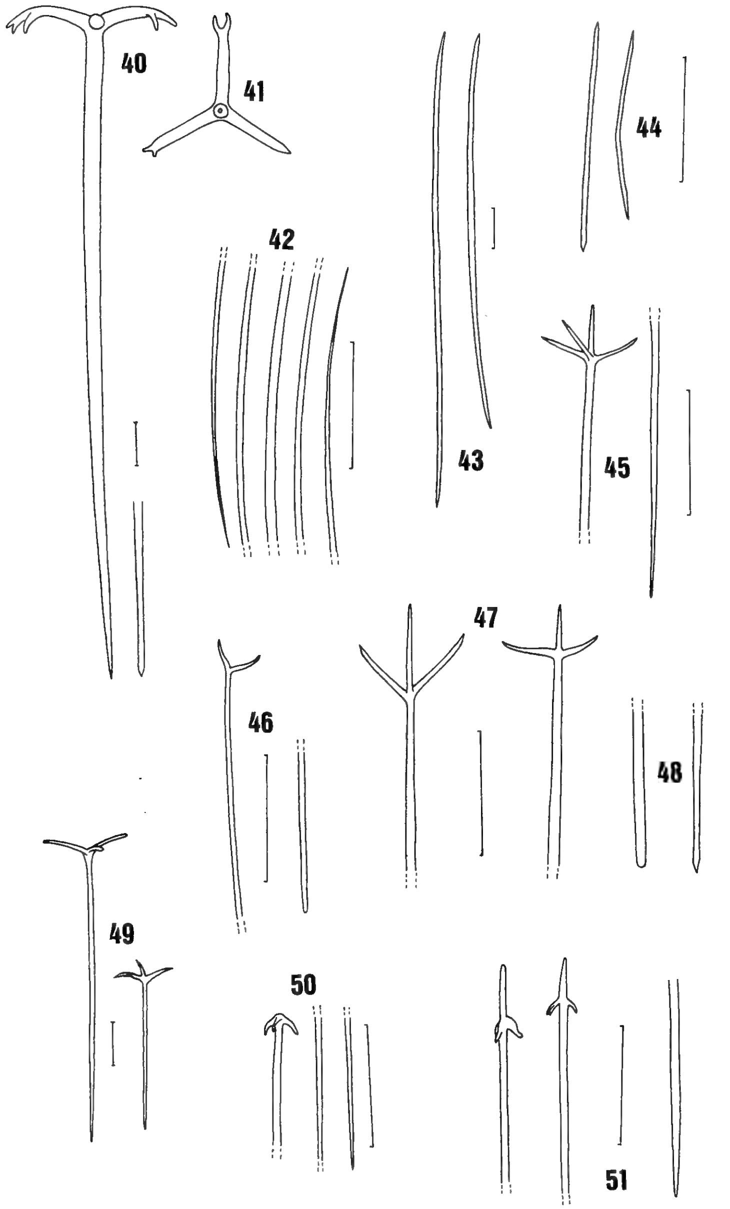
Anatriaenes (fig. 50): rare (N=6); straight rhabd with gradually pointed ends, cladi with gradually pointed or strongyliform ends, length 4501 µm, width 9.5-12.3 (m, cladome diameter 33-67 µm, cladi length 19-38 µm, cladi thickness at the base 6.6-9.5 µm.

Plagiotriaenes (fig. 49): rare (N=4); straight rhabd with gradually pointed end; cladi gradually pointed, length 1495-1886 µm, width 28-39 µm, cladome diameter 460-506 µm, cladi length: 230-253 µm, cladi thickness at the base 23-37 µm.

Protriaenes (figs 47, 48): rare (N=6), straight or slightly curved rhabd, with blunt or abruptly pointed end, length 3030-5282 µm, width: 9.5-19 µm; cladome diameter 95-204.2 µm, cladi length 62-124 µm, cladi thickness at the base 8.5-14.2 µm.

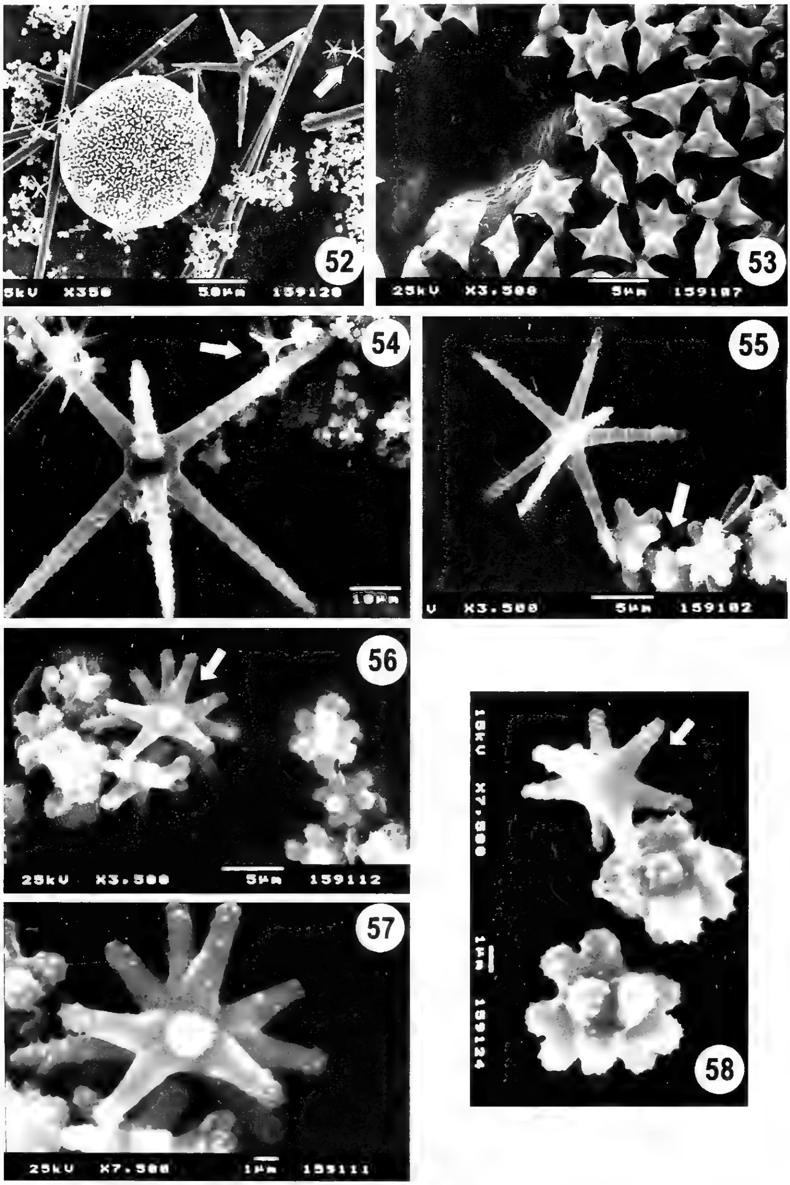
Anamesotriaenes (fig. 51). rare (N=5); straight rhabdome with abruptly pointed or strongyliform end; cladi with conical or strongyliform ends, length 5938-7581 µm, width 9.5- 14.2 µm, cladome diemeter 49-67 µm, cladi length 19-38 µm, cladi thickness at the base 6.7- 14.2 µm.

Promesotriaenes (fig. 45): rare (N=3); straight rhabdome with gradually pointed end; cladi with gradually pointed or strongyliform end, length 2484-3404 µm, width 9.5-19 µm, cladome diameter 105-190 µm, cladi length 52-105 µm, cladi thickness at the base 9.5-16.1 µm.



FIGS 40-51

Megascleres of *Geodia riograndensis* sp. n.: 40, orthotriaene; 41, orthotriaene cladome in apical view; 42, oxea I; 43, oxeas II; 44, oxeas III; 45, promesotriaene; 46, diaene; 47, protriaene; 48, protriaene basal extremity; 49, plagiotriaene; 50, anatriaene; 51, anamesotriaene. Scales = 200 µm.



FIGS 52-58

Microscleres of *Geodia riograndensis* sp. n.: 52, sterraster, oxyaster I and oxyaster II (arrow); 53, sterraster surface with hilum; 54, oxyaster I and II (arrow); 55, oxyaster II e spherostrongylaster (arrow); 56, strongylaster and spherostrongylaster (arrow); 57, strongylaster; 58, strongylaster (arrow) and spherostrongylaster.

Diaenes (fig. 46) : rare (N=2); straight or slightly sinuous rhabdome, with gradually pointed end, length 184 µm, width 17 µm, cladome diameter 200 µm, cladi length 157 µm, cladi thickness at the base 13.3 µm.

Sterrasters (figs 52, 53): spherical or oval; hilum spherical and conspicuous; surface provided with irregular microspines in form of a rosette, sometimes absent in the region around the hilum: diameter 57-*98.1*-124 µm/48-*89.9*-114 µm.

Oxyasters I (figs 52, 54): 3 to 8 microspined rays distributed along its whole length, diameter 64-*86,4*-117 µm, center: 5.7-*8.3*-11.5 µm, rays length 30-*41.9*-58 µm, rays width 2.3-*3.8*-4.6 µm.

Oxyasters II (figs 52, 54, 55): 4 to 9 microspined rays at the distal portion or, more rarely, all along their length, diameter 14-*20.2*-30 µm, center 1.8-*3.0*-4.6 µm, rays length 4.6-*9.0*-13.8 µm, rays width 1.1-*1.6*-2.3 µm.

Strongylasters (figs 56-58) - varying to spherostrongylasters (figs 55, 56, 58). 5 to 13 rays with strongyliform or truncate ends, microspined all along their length or, more rarely, at the distal half, diameter 4.6-*8.4*-13.2 µm, center 1.6-*3.2*-4.6 µm, rays length: <1.0-*3.0*-4.6/≤ 1.0 µm.

Etymology: The specific name refers to the Rio Grande do Sul State coast, off which the sponges were collected.

Remarks: When compared with other species of *Geodia* from the Brazilian coast, *Geodia riograndensis* sp. n. is close to *G. glariosa* Sollas, 1886 [Syntype BMNH 1889.1.1.86] by the shared occurrence of oxeas, ortho-, pro- and anatrienes as megascleres, differing, however, for presenting additional categories of megascleres, as three categories of oxeas, plagiotriaenes, anamesotriaenes, promesodiaenes, promesotriaenes and diaenes; and of microscleres, as oxyasters, strongylasters and strongylospherasters.

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Oribatids from Switzerland III (Acari: Oribatida: Oppiidae 1 and Quadroppiidae). (*Acarologica Genavensia* XCIII)

Sándor MAHUNKA & Luise MAHUNKA-Papp
Zoological Department, Hungarian Natural History Museum, Baross utca 13, H-1088 Budapest, Hungary.

Oribatids from Switzerland III (Acari: Oribatida: Oppiidae 1 and Quadroppiidae). (*Acarologica Genavensia* XCIII). – Oppioid oribatids taken from soil samples in Switzerland are recorded. There are 15 species, of which 6 are new for science and one of them also represents a new genus: *Paramedioppia* gen. n. (Oppiidae). The following 5 new combinations are proposed: *Berniniella conjuncta* (Strentzke) comb. n. et stat. n. = *Oppia sigma conjuncta* Strentzke, 1951; *Berniniella hauseri* (Mahunka) comb. n. = *Oppia hauseri* Mahunka, 1974; *Berniniella serratirostris* (Golosova) comb. n. = *Oppia serratirostris* Golosova, 1970; *Dissorhina signata* (Schwalbe) comb. n. = *Oppia signata* Schwalbe, 1989; *Lauroppia maritima* (Willmann) comb. n. = *Oppia maritima* Willmann, 1929; 1 species is placed in synonymy: *Oppiella rafalskii* Opłotna & Rajski, 1983 = *Berniniella hauseri* (Mahunka, 1974): syn. n. In addition 2 species (still not recorded for Switzerland) are discussed, in this way a total of 17 oppioid species are considered. Morphological and distributional data of 11 species are provided and the nature of relationships and some additional morphological characters are discussed.

Key-words: Acari - Oribatida - Oppiidae - Quadroppiidae - taxonomy - new species - new genus - new combinations - Switzerland.

INTRODUCTION

Our revision work regarding the oribatids of Switzerland, which will eventually be incorporated into a book, has several times been mentioned (e.g. Mahunka, 1993, 1996a). For the very simple reason that at least another 4-5 years will have to elapse until the appearence of this book, we believe that all the taxonomic novelties and specific faunistic data should be published in order to complement the ever increasing number of taxonomic and zoogeographic researches. This time we propose to discuss a part of the available information gained in connection with species belonging to the superfamily of Oppioidea.

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We should stress that, in referring to the taxon superfamily, we adopt the system incorporating e.g. the following families: Oppiidae, Quadroppiidae and Suctobelbidae. In this paper we discuss especies belonging to the families Oppiidae Grandjean, 1951 and Quadroppiidae Balogh, 1983. The subfamilial division within the family Oppiidae seems quite unsuitable for further subdivisions, especially since there are many genera (see Mahunka, 1999).

List of localities

GE-4 = Switzerland: Genève: Frontenex, pieds souches chênes; 14.VII.1980; leg. C. Besuchet – (33).
GR-6 = Switzerland: Graubünden: Landquart, pieds aulne (*Alnus*); 26.IX.1983; leg. C. Besuchet – (118).
GR-8 = Switzerland: Graubünden: Samnaun, alpine Wiesen mit *Rhododendron*, Gesiebe, 2050m; 26.VIII.1968; leg. C. Besuchet – (26).
GR-9 = Switzerland: Graubünden: Santa Maria – Paß Umbrail, Gesiebe, 2000m; 5.VIII.1974; leg. C. Besuchet – (37).
GR-10= Switzerland: Graubünden: Untervaz b. Chur, mousses; 29.IX.1983; leg C. Besuchet – (126).
LU-1 = Switzerland: Luzern: Eigenthal, près Eigenthal (village) Forenmoos, *Sphagnum*, 970m.; 2.VIII.1996; leg. C. Besuchet – (108).
NW-1 = Switzerland: Nidwald: Musenalp, oberhalb Niederrickenbach, mousses dans lappiaz, 1800m; leg. C. Besuchet – (113).
NW-2 = Switzerland: Nidwald: Pilatus, tamisage rhododendron, 1800m; 14.VI.1984; leg. I. Löbl – (123).
NW-3 = Switzerland: Nidwald: Trübsee, mousses près source, 1800m; 8.IX.1997; leg. C. Besuchet – (127).
SO-5 = Switzerland: Solothurn: Schottwill, Bucheggberg, Rindenmoos von lebendem Baum; 27.IX.1987; leg. S. Mahunka & L. Mahunka-Papp – (47).
SZ-3 = Switzerland: Schwyz: Pragelpaß, mousses sapins, 1650m; 25.VIII.1983; leg. I. Löbl – (116).
TI-5 = Switzerland: Tessin: Monadello - Moneto, im faulenden Laub, 850m; 23.IV.1992; leg. C. Besuchet – (91).
TI-9 = Switzerland: Tessin: Nufenen-Paß, Boden, dürres Laub und Baummulm aus einem Lärchenwald; 15.VI.1979; leg. S. Mahunka & L. Mahunka-Papp – (18).
TI-11 = Switzerland: Tessin: Rancate, forêt de châtaigniers, tamisages; 7.IX.1965; leg. C. Besuchet – (25).
VS-4 = Switzerland: Valais: Daubensee, mousses et herbes, 2200m; 11.VIII.1980; leg. C. Besuchet – (32).
VS-8 = Switzerland: Valais: Forêt de Finges, souches pins (*Pinus*); 14.VIII.1980; leg. C. Besuchet – (5).

LIST OF IDENTIFIED SPECIES

OPPIIDAE Grandjean, 1951

Berniniella conjuncta (Strentzke, 1951) comb. et stat. n.
Locality: NW-2.
Distribution: Germany; first record for Switzerland.

Berniniella hauseri (Mahunka, 1974) comb. n.
Localities: GR-6; TI-11.
Distribution: Europe; first record for Switzerland.

Dissorhina signata (Schwalbe, 1989) comb. n.
Locality: GR-9.
Distribution: Germany (known from the type locality only); first record for Switzerland.

Lauroppia hauseri sp. n.
Localities: TI-5; TI-11.

Lauroppia maritima (Willmann, 1929) comb. n.
Localities: SO-5; TI-9.
Distribution: Palearctic Region; first record for Switzerland.

Lauroppia obscura sp. n.
Localities: GR-8; VS-4; VS-8.

Moritzoppia incisa sp. n.
Localiy: NW-3.

Moritzoppia keilbachi (Moritz, 1969)
Locality: SZ-3.
Distribution: Europe; first record for Switzerland.

Oppiella besucheti sp. n.
Locality: SZ-3.

Oppiella propinqua sp. n.
Locality: LU-1.

Oxyoppioides decipiens (Paoli, 1908)
Locality: GE-4.
Distribution: Central and Southern Europe, Caucasus; first record for Switzerland.

Paramedioppia helvetica gen. n., sp. n.
Locality: TI-9.

Subiasella quadrimaculata (Evans, 1952)
Locality: GR-10.
Distribution: Europe; first record for Switzerland.

QUADROPPIIDAE Balogh, 1983

Quadroppia longisetosa Mínguez, Ruiz & Subías, 1985
Locality: NW-1.
Distribution: Southern Europe; first record for Switzerland.

Quadroppia michaeli Mahunka, 1977
Locality: not recorded for Switzerland.
Distribution: Greece and Spain.

Quadroppia omodeoi Mahunka & Paoletti, 1984
Locality: not recorded for Switzerland.
Distribution: Italy.

Quadroppia cf. *paolii* Woas, 1986
Locality: GR-10.
Distribution: Palearctic Region; first record for Switzerland.

DESCRIPTION AND REDESCRIPTION OF SOME OF THE OPPIOID SPECIES

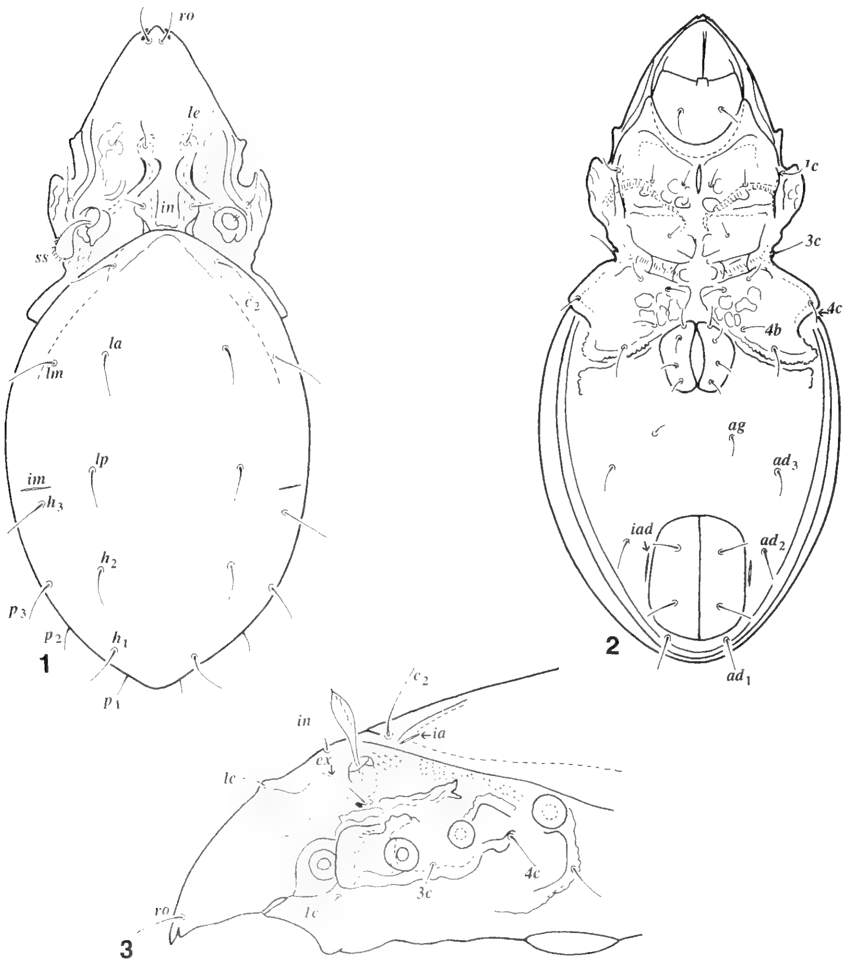
The present paper records 15 species belonging to the superfamily Oppioidea Grandjean, 1951 found in the territory of Switzerland (13 species of the family Oppiidae and 4 species of the family Quadroppiidae). In exceptional cases we also discuss species unrecorded in Switzerland so far, when it is deemed important to elucidate certain specific taxonomic questions. Among the species 6 are new for science and 1 represents a new genus (*Paramedioppia*). In addition some extremely rare species are touched upon. Morphological complementations, corrections, new combinations, the publication of synonyms and the reinterpretation of some species are also given.

Berniniella conjuncta (Strenzke, 1951) comb. et stat. n. Figs 1-3

Oppia sigma conjuncta Strenzke, 1951: 723, fig. 5.
Oppiella sigma (Strentzke, 1951): sensu Woas, 1986: 182, Abb. 88-89.

Material examined: Switzerland: NW-2.

Remarks: The recently examined soil samples harboured, in many cases, the very same species which we could readily identify with the description of Strenzke's *Oppia sigma conjuncta* published in 1951, and with Woas's redescription



FIGS 1-3

Berniniella conjuncta (Strenzke, 1951) – 1: body in dorsal view, 2: body in ventral view, 3: podosoma in lateral view.

of *Oppia sigma* published in 1986. Without doubt Strenzke's description is inadequate since the description of the ventral side is missing. However, on the basis of the Swiss specimens and the redescription of Woas now we may safely conclude that *O. conjuncta* is an independent, valid species. Furthermore, we should like to point out that Woas made a mistake when preparing his redescription, since his specimens belong to *O. conjuncta* and not to *O. sigma*.

The drawings were made from the specimens originating from Switzerland which readily correspond with the figures of both Strenzke and Woas. For this reason a complete redescription would be out of place here. Nevertheless, we should like to draw the attention to some important features.

Measurements: Length of body: 208-224 μm, width of body: 102-114 μm.

Dorsal side (Fig. 1): Rostrum with wide median apex, lateral apices much smaller. Costulae S-shaped, directed to the bothridia. One pair of median laths directed outwards, not connecting with the costulae. Bothridium with posterior tubercle, behind it comparatively large pustules are evident. Sensilli with short bristles. Dorsosejugal suture protruding anteriorly, ten pairs of notogastral setae nearly equal in length.

Lateral part of podosoma (Fig. 3): Well sclerotized, longitudinal crests and pustulated or granulated fields are visible. Ratio of prodorsal setae: $ro \approx ex > in \approx le$. Setae *1c* do not arise on pedotecta I, discidium well developed bearing setae *4c*.

Ventral side (Fig. 2): Sternal apodemes and borders weakly developed or absent. Sejugal apodemes with longitudinal, arched lines in opposite position. Posterior margin of epimeral borders 2 and 4 undulate or denticulate. Epimeres 1 framed laterally by longitudinal crests bearing setae *1c* anteriorly. Anogenital setal formula: 4 - 1 - 2 - 3. All setae in the epimeral and anogenital region simple, setiform, without conspicuous cilia.

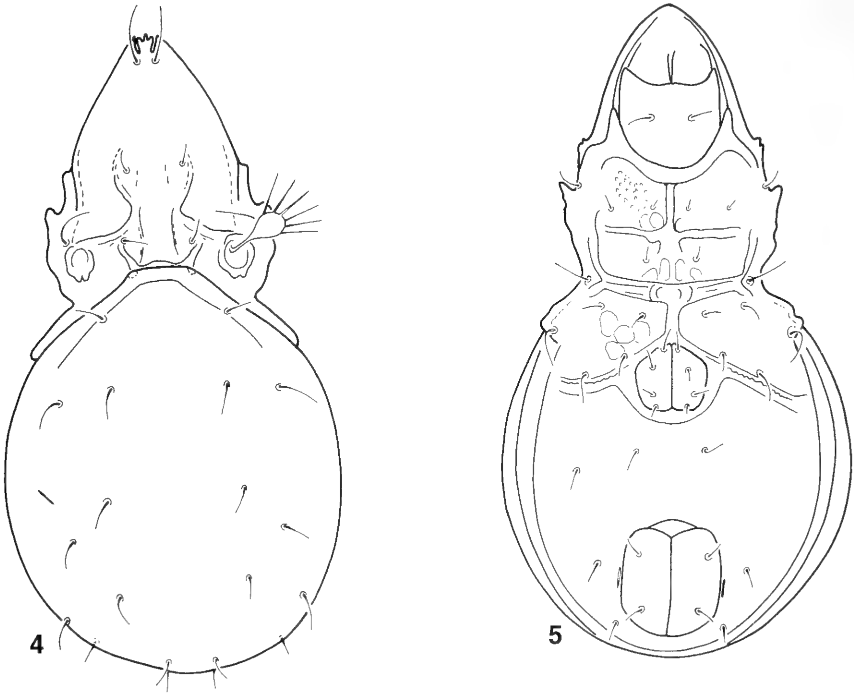
Berniniella hauseri (Mahunka, 1974) comb. n. Figs 4-5

Oppia hauseri Mahunka, 1974: 585, Abb. 34-36.
Oppiella rafalskii Opłotna & Rajski, 1983: 543, figs 1-8. Syn. n.

Material examined: Switzerland: GR-6; T-11.

Remarks: The recently collected specimens are quite identical with those described from Greece (Mahunka, 1974). However, the ventral side was not described, so the relegation of the species was only provisional owing to lack of information regarding the number of genital setae and some other ventral features. After having again examined the type species we found, as it was expected from the dorsal side, that *O. hauseri* has 4 pairs of genital setae corresponding well in all other features with those of specimens collected recently in Switzerland. One of these was selected for the drawings (Figs 4-5).

Taxonomic position: After examining the related species, it is certain that *Berniniella serratirostris* (Golosova, 1970) comb. n. and *Berniniella*



FIGS 4-5

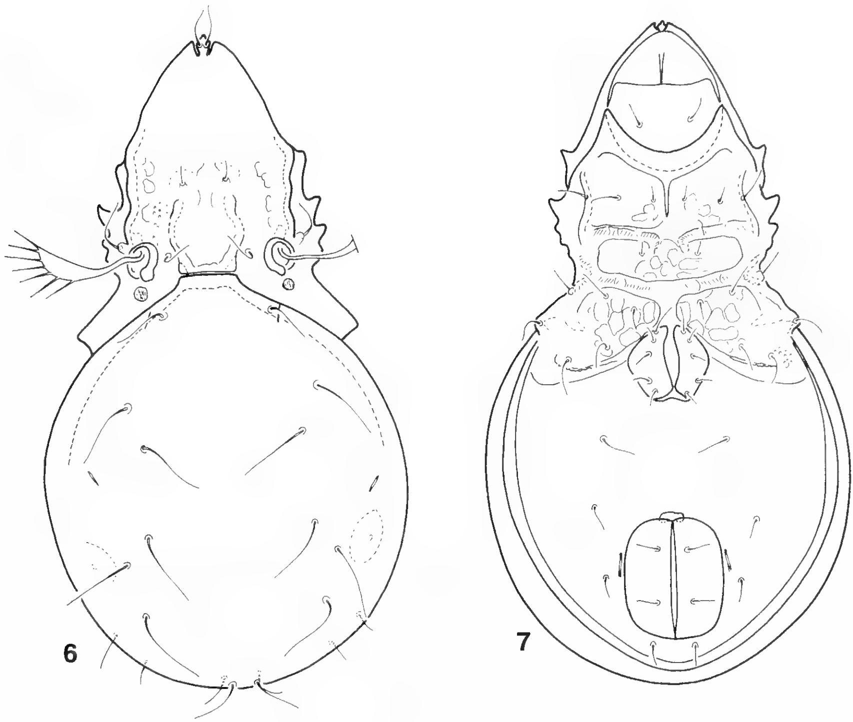
Berniniella hauseri (Mahunka, 1974) – 4: body in dorsal view, 5: body in ventral view.

rafalskii (Opłotna & Rajski, 1983) comb. n. are its closest allies. Peculiarly enough, we could not find any differentiating character between the latter and *B. hauseri*, thus, we consider them synonyms; so the latter is a junior synonym of *B. hauseri*. The authors' description - besides the obvious mistakes - is wholly identical with the features of the Swiss specimens. The only difference we could ascertain stems from the drawing technique, due to some simplified method used by the authors. Thus, the median part of the dorsosejugal region, the costula on the basal part of the prodorsum and also the median thickening are figured to be more complicated than they in fact are. A similar problem is found with the drawing of the sejugal borders and the coxisternal region. The position of setae *2b*, *2c* and *3c* is obviously erroneously depicted. Opłotna & Rajski (1983) thoroughly evaluated the relationship of *Oppia serratirostris* with *Oppiella rafalskii*. These differences (especially the number of branches of the sensilli, the shape of the costulae and the shape of the median rostral apex) are convincing enough for us, too.

Dissorhina signata (Schwalbe, 1989) comb. n. Figs 6-9

Oppia signata Schwalbe, 1989: 99, Abb. 1.

M a t e r i a l e x a m i n e d : Switzerland: GR-9.



6

7

Figs 6-7

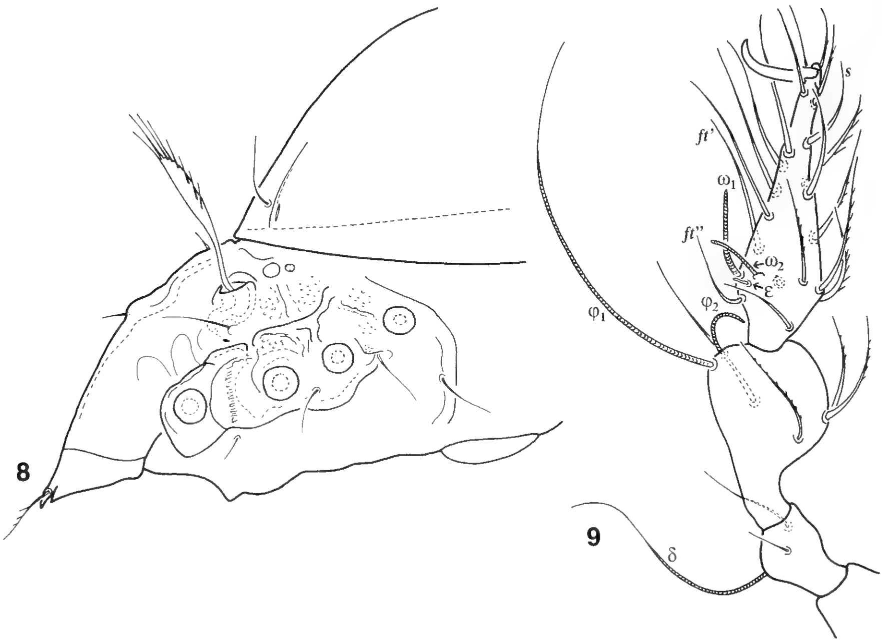
Dissorhina signata (Schwalbe, 1989) – 6: body in dorsal view, 7: body in ventral view.

R e m a r k s : On the basis of the sensillar shape and its unilateral ciliation, the species of the genus *Dissorhina* Hull, 1916 may grouped into two. The "*ornata* species group" has bacilliform sensilli, whose distal end is spiculate or quite smooth, while the "*tricarinatoides* species group" has sensilli with very long unilaterally arranged branches. The studied species belongs to the second group.

R e d e s c r i p t i o n : The specimens of this species collected in Switzerland have been stored for some time in the Geneva collection. These specimens are easily identifiable with the description and the given figures. Some important features which deserve special attention are described below.

M e a s u r e m e n t s . – Length of body: 197-208 µm, width of body: 103-134 µm.

D o r s a l s i d e (Fig. 6): Rostrum tripartite, rostral setae arising exactly on the triangular, well separated median apex. Costulae casket-shaped, diverging medially and converging distally. Lamellar setae arising on small separated parts. Bothridium with a posterior tubercle, behind it a well developed, separated, round tubercle. Sensilli with 6-7 long, branches unilaterally. Dorsosejugal suture well protruding anteriorly, with a straight median part. Ten pairs of notogastral setae nearly equal in length. Setae c_2 not shorter than the others.



Figs 8-9

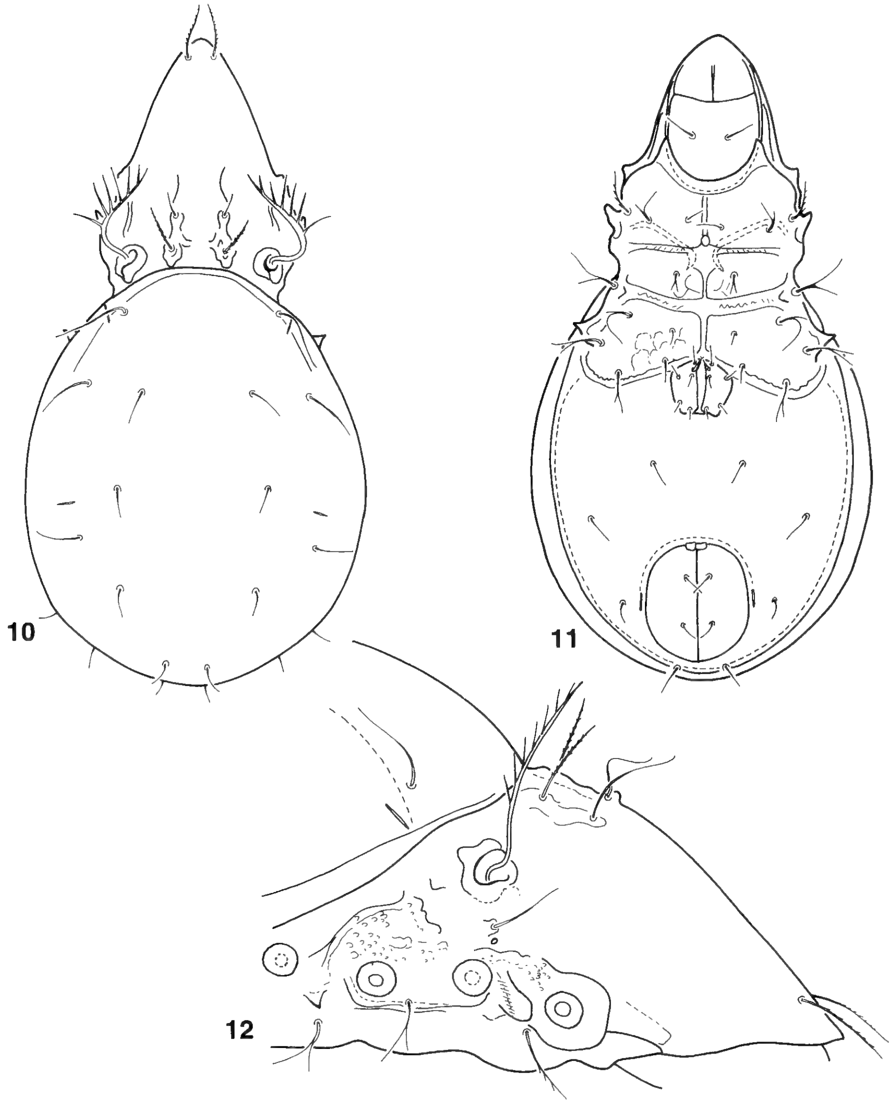
Dissorhina signata (Schwalbe, 1989) – 8: podosoma in lateral view, 9: leg I.

Lateral part of podosoma (Fig. 8): Well sclerotized, longitudinal crests and pustulated or granulated fields are visible. Ratio of prodorsal setae: *ro* ≈ *ex* > *in* ≈ *le*. Setae *1c* do not arise on pedotecta I, discidium well developed and bearing setae *4c*.

Ventral side (Fig. 7): Sternal apodemes absent between *bo*. 2 and *bo. sej*. Sejugal apodemes with longitudinal, arched lines. Posterior margin of epimeral borders 4 undulate or denticulate. Epimeres 1 framed laterally by longitudinal crests bearing setae *1c*. Anogenital setal formula: 5 - 1 - 2 - 3. All setae in the epimeral and anogenital region simple, setiform, without conspicuous cilia.

Legs: Form and chaetotaxy of leg I as shown in Fig. 9.

Taxonomic position: The species *D. signata* stands very near to *D. tricarinatoides* (Dubinina, *in* Dubinina *et al.* 1966) (see also Mahunka, 1996b). It may be distinguished by the shape of the prodorsal costulae with the auxiliary complementary ribs, which are present in *D. tricarinatoides* and absent in *D. signata*, and the position of setae ad_3 which arise nearer to the anal plates than the lateral margin of ventral plate in *D. signata* (much farther, near to the lateral margin in *D. trticarinatoides*).



FIGS 10-12. *Lauroppia hauseri* sp. n. – 10: body in dorsal view, 11: body in ventral view, 12: podosoma in lateral view.

Lauroppia hauseri sp. n. Figs 10-12

Material examined: Switzerland: Holotype: Tessin: TI-11, 1 paratype from the same sample; 6 paratypes: Tessin: TI-5. Holotype and 4 paratypes: MHNG[1], 3 paratypes (1614-PO-98): HNHM[2].

[1] MHNG: deposited in the Muséum d'histoire naturelle, Geneva.
[2] HNHM: deposited in the Hungarian Natural History Museum, Budapest, with identification number of the specimens in the Collection of Arachnida.

Diagnosis: Rostrum elongated, rostral apex roundish. Short, basally dilated, guttiform costulae present Sensilli pectinate. Median part of the anterior notogastral margin straight. Ten pair of notogastral setae, setae c_2 long. Six pairs of genital setae, anogenital region normal.

Measurements: Length of body: 369-443 µm, width of body: 188-214 µm.

Prodorsum: Rostral part of prodorsum conspicuously elongated, rostral apex conical, rounded medially. Prodorsal surface with short basal transcostulae protruding from the guttiform basal tubercles. Bothridia well developed, with conspicuously large basal tubercles. Rostral setae arising from the rostral surface, lamellar setae located very far from the rostrals, near to the interlamellar setae. Lamellar setae fine, setiform, arising at the distal end of the costulae, interlamellar setae much thicker, ciliate, straight, arising from the guttiform tubercles. Sensilli pectinate, directed forwards, each bearing 7 branches unilaterally.

Lateral part of podosoma: Sejugal region covered by a thick cerotegument layer. Surface weakly granulated, with larger pustules between the acetabula. Acetabula IV placed above acetabula I-III. Setae *1c* arising near to small pedotecta I (Fig. 12).

Notogaster: Anteromedian margin of notogaster straight, not penetrating between the bothridia. A weak crista present. Ten pairs of notogastral setae present, setae c_2 long, longer than the others. Setae *la* arising in front of *lm* (Fig. 10). Setae *la* and h_3 longer than the remaining ones, setae p_1, p_2, and p_3 shortest of all.

Ventral side (Fig. 11): Apodemes and borders weakly developed, epimeral surface ornamented by a weak polygonal design. Posterior border of epimeral region undulate or denticulate. Epimeral setae partly ciliate or bifurcate. Lateral setae (*3c*, *4c*) longer than the inner ones. Anogenital setal formula: 6 - 1 - 2 - 3. All setae in anogenital region simple and short.

Remarks: On the basis of the prodorsal structure and the basal position of the lamellar and interlamellar setae the new species belongs to the "*fallax*-group" (see Willmann, 1931). The new species is distinguished from its congeners by the ratio and form of the prodorsal setae and the very short h_1 and p setae.

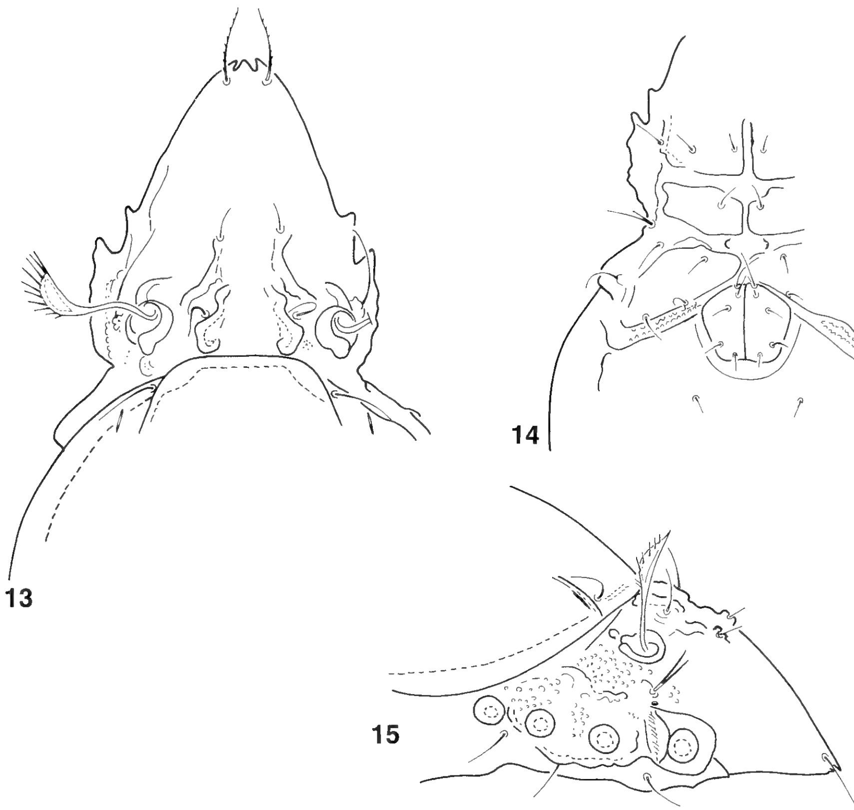
Derivatio nominis: We dedicate the new species to our friend, Dr. B. Hauser, the initiator of the "Oribatida Helvetica project".

Lauroppia maritima (Willmann, 1929) comb. n. Fig. 13-15

Oppia maritima Willmann, 1929: 45, Abb. 4.
Oppia maritima: Strenzke, 1951: 720, fig. 2

Material examined: Switzerland: SO-5; TI-9.

Remarks: The species was described by Willmann (1929), and Strenzke (1951) redescribed it. Both these descriptions are inadequate and some very important features are missing. Therefore, we give herewith some drawings and a short description.



FIGS 13-15

Lauroppia maritima (Willmann, 1929) – 13: prodorsum in dorsal view, 14: epimeral region, 15: podosoma in lateral view.

P r o d o r s u m : Rostral apex sharply pointed, the incisure wide, lateral apices much smaller than the median one (Fig. 13). Exobothridial setae bifurcate. Exobothridial region well sclerotized (Fig. 15), surface around the bothridia and acetabulae I-IV pustulate or granulate.

N o t o g a s t e r : Protruding anteriorly, however, the median part of the dorsosejugal line is straight.

V e n t r a l s i d e : Posterior border of the coxisternal region with pustulate margin, pustules are in a transversal hollow on both sides (Fig. 14). Setae *1c* arising far from pedotecta I. Setae *3c* bifurcate. Anogenital setal formula: 5 - 1 - 2 - 3. Anterior pair of genital setae much longer than the others.

Lauroppia obscura sp. n. Figs 16-20

Material examined: Switzerland: Holotype: Valais: VS-8, 6 paratypes from the same sample; 4 paratypes: Valais: VS-4; 6 paratypes: Graubünden: GR-8. Holotype and 10 paratypes: MHNG, 6 paratypes (1615-PO-98): HNHM.

Diagnosis: Rostrum divided by two incisions, median apex triangular. Prodorsum with complicate costulae. Sensilli clavate, unilaterally spinose. Notogaster straight anteriorly. Ten pairs of notogastral setae, c_2 long. 5 pairs of genital setae, anogenital region normal.

Measurements: Length of body: 280-305 µm, width of body: 148-172 µm.

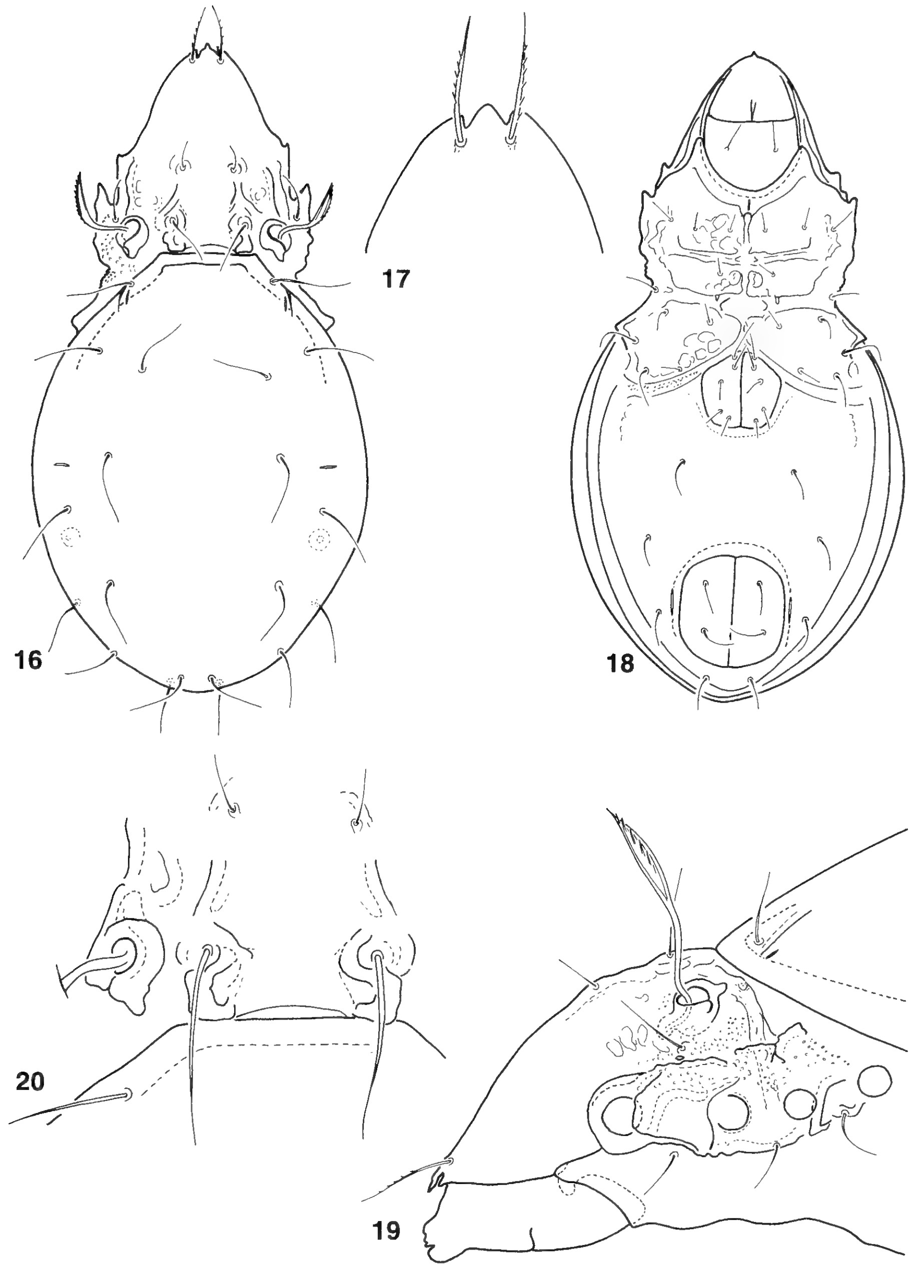
Prodorsum: Rostral apex (Fig. 17) divided by two small incisions, median apex conspicuously wide, sometimes triangular, or blunt at tip, sometimes its margin undulate. Lateral apices with simple, sharp points. Among the costulae one pair arched and comparatively well developed, they do not reach the bothridium or the bases of the lamellar setae. A pair of S-shaped basal costulae also present reaching to the inner margin of the longitudinal ones (Fig. 20). Lateral part of prodorsum well sclerotized, with some tubercles and pustules, one pair of which bears the exobothridial setae. In the dorsosejugal region one pair of indistinct porose areas also visible (Fig. 19). Bothridia large with strong posterior apophyse. Rostral setae arising dorsally, comparatively near to each other. Lamellar setae shorter than the other prodorsal setae, arising on small tubercles independently of the longitudinal costula. Sensilli elongate, their head asymmetrically clavate, with short spines on their outer margin.

Lateral part of podosoma: Exobothridial region and fields between acetabula I - IV granulated by comparatively large granules or pustules. Some well-sclerotised, long, longitudinal crests also present. A pair of porose areas in the sejugal region. Positions of acetabula III and IV nearly the same as those of acetabula I and II (Fig. 19). Pedotecta I small, setae *1c* arising far from its basal part. Discidium well developed, setae *4c* arising far from its lateral margin, on the epimeral surface.

Notogaster: Elongated, dorsosejugal part straight anteriorly. Crista clearly seen. Ten pairs of notogastral setae present, setae c_2 conspicuously long, setiform, all others somewhat shorter. Setae *lm* arising in front of *la* (Fig. 16). Setae p_1, p_2 and p_3 only slightly shorter than the others.

Ventral side (Fig. 18): Epimeral region hardly sclerotised. Apodemes partly absent only borders visible between the borders 2 and sejugal borders or sejugal borders and borders 4. Lateral borders on epimeres 1 arched bearing setae *1c*. Sejugal borders broad, with a pair of hollows medially, with similar, but smaller ones, also present on *bo* 2. All epimeres with a polygonal pattern. Setae *4c* arising on the epimeral surface. Epimeral setae long, simple. Anogenital setal formula: 5 - 1 - 2 - 3. Among the genital setae the two anterior pairs conspicuously long, directed forwards. Position and shape of the aggenital, anal setae and lyrifissures *iad* normal.

Legs: Solenidia of tibia IV very long and curved .



FIGS 16-20

Lauroppia obscura sp. n. – 16: body in dorsal view, 17: rostrum, 18: body in ventral view, 19: podosoma in lateral view, 20: basal part of prodorsum.

Remarks: On the basis of the form and structure of the prodorsum the new species belongs to the *L. maritima* group. Although closely related to *L. maritima*, the head of the sensillus of the new species is much longer and the spines on the sensillar head are very short (long in *L. maritima*).

Derivatio nominis: Named after the complicated prodorsal design and rostral apex.

Moritzoppia incisa sp. n. Figs 21-23

Material examined: Switzerland: Holotype: Nidwald: NW-3, 26 paratypes from the same sample. Holotype and 16 paratypes: MHNG, 10 paratypes (1613-PO-98): NHMH.

Diagnosis: Rostrum roundish. Prodorsum with complicate costulae. Sensilli clavate, unilaterally pectinate. Anterior margin of notogaster protruding into the interbothridial region and interrupted medially. Cristae present. Ten pairs of notogastral setae, setae c_2 long. Four pairs of genital setae, anogenital region normal.

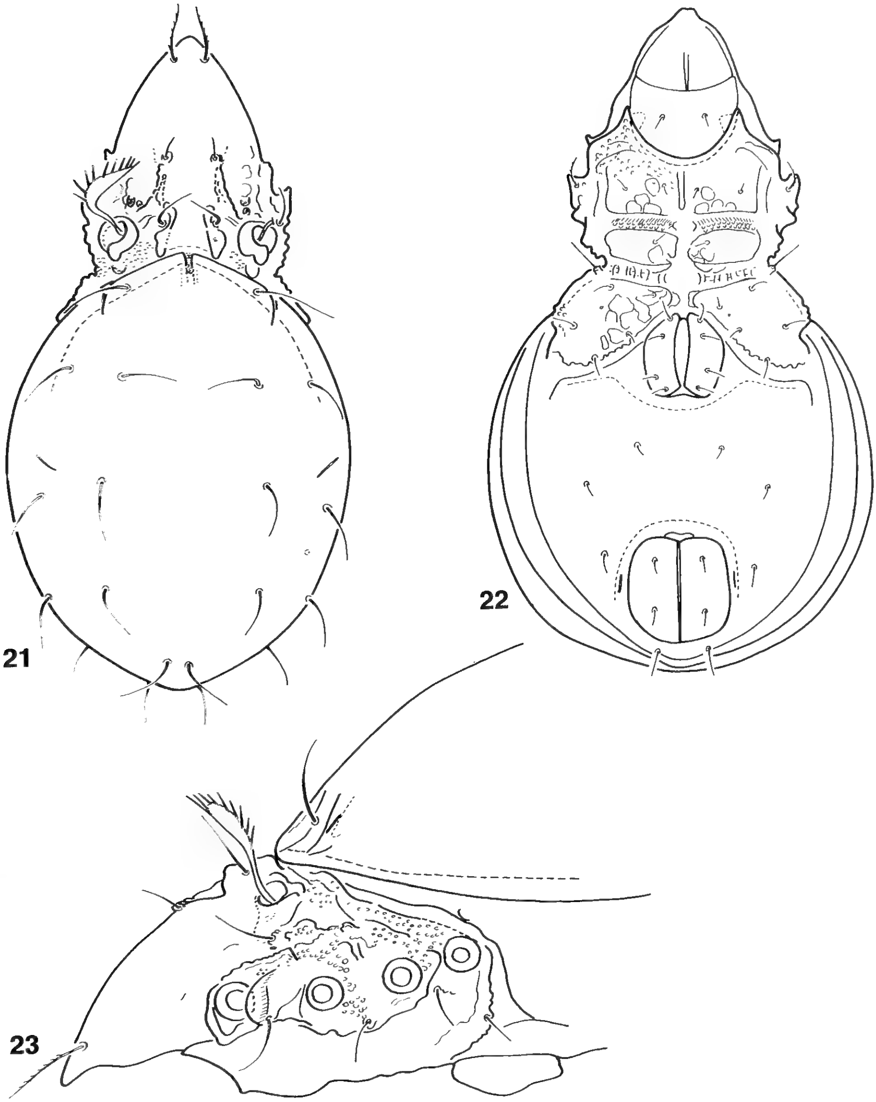
Measurements: Length of body: 267-276 µm, width of body: 152-155 µm.

Prodorsum: Rostrum slightly elongated, with nasiform median apex. Lamellar costulae weakly sclerotized, lamellar apices usually separated, their anterior part carrying some pustules. A pair of elongated, guttiform tubercles in the interbothridial region bearing interlamellar setae at their outer margin. A pair of round tubercles present in the middle part of the costulae, they are opposed on both sides (Fig. 21). Some weak sigillae visible laterally. Bothridia well developed, with large basal tubercles surrounded with a granulated field. Rostral setae arising on the dorsal surface, ciliate. Lamellar setae arising on the lamellar apices. The ratio of the prodorsal setae: $ro > in \approx ex > le$. Sensilli with well developed heads, bearing 9-10 branches unilaterally.

Lateral part of podosoma: Well sclerotized, nearly the whole surface well granulated and/or pustulate. Large pustules present also above the acetabula of legs III and IV (Fig. 23). Some longitudinal crests also present. Ventral border especially undulate and incised, acetabula I-IV arranged nearly in a longitudinal line. No porose area visible behind the bothridia.

Notogaster: Dorsosejugal part of the notogaster protruding anteriorly in the interbothridial region. Crista present laterally. Dorsosejugal margin interrupted medially and framed by a pair of short crests directed posteriorly, sometimes some spots are visible in this slit. Ten pairs of notogastral setae present, setae c_2 slightly longer than the others, *la*, *lm* and *lp* equal in length, setae *h* and setae *p* only slightly shorter.

Ventral side (Fig. 22): Well sclerotized, all apodemes and borders well developed. Lateral margin of epimeres 1 framed by longitudinal borders, but setae *1c* arising on pedotecta I. The surface of epimeres I pustulate, posterior borders also conspicuously covered by granules or pustules. Sejugal borders with some pairs of longitudinal crests or lines. Posterior margin of borders IV strongly undulate. Setae *4b* arising at the posterolateral corner. Surface around discidium also pustulate. Setae *4c*



FIGS 21-23
Moritzoppia incisa sp. n. – 21: body in dorsal view, 22: body in ventral view, 23: podosoma in lateral view.

stand further from the discidia. All epimeral setae simple and smooth. Anogenital setal formula: 4 - 1 - 2 - 3. All setae simple. Lyrifissures *iad* short, located in paraanal position.

R e m a r k s : On the basis of the structure of the dorsosejugal margin of the notogaster, the new species is distinguished from all congeners.

D e r i v a t i o n o m i n i s : Named after the incised anterior margin of the notogaster.

Moritzoppia keilbachi (Moritz, 1969)

Oppia keilbachi Moritz, 1969: 37, Abb. 1-3.
Moritziella keilbachi: Balogh, 1983: 26, 9: 9p-v.
Moritzoppia keilbachi: Subías & Rodriguez, 1988: 122.

M a t e r i a l e x a m i n e d : Switzerland: SZ-3.

R e m a r k s : The species was described by Moritz (1969) on the basis of females. A male specimen has been found in the Swiss material. The habitus of the male is more slender and it is also smaller (210µm x 92 µm) than the female. In all other features it corresponds well with the original description and the figures. Especially important is the granulate surface behind the bothridium and on the discidium and the shape of the sensillus. The sensillus of the studied individual is blunt at tip, its head bearing simple, short cilia, arranged in 2-3 rows. Features of the ventral region also accord well with the original description, e.g. the posterior borders of the coxisternal region have an undulate margin.

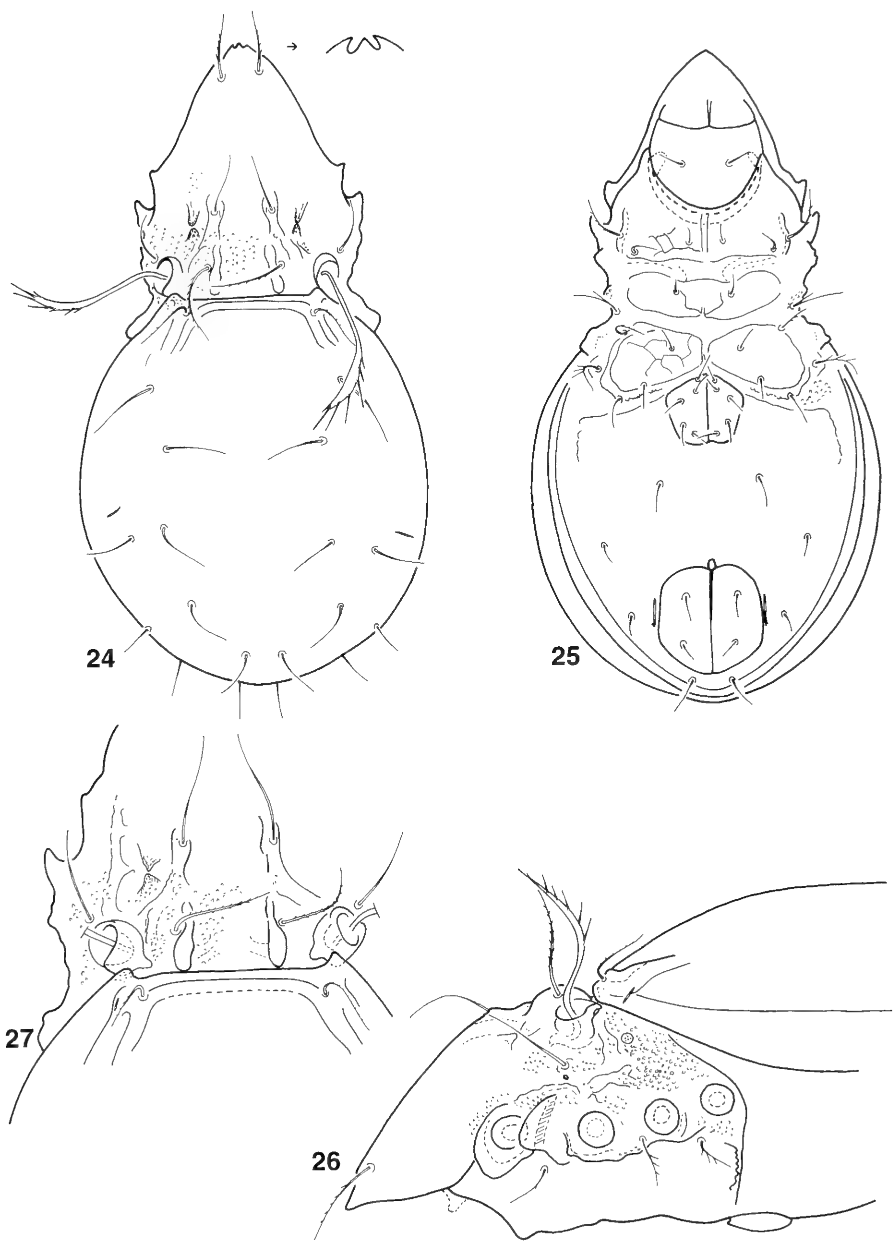
Oppiella besucheti sp. n. Figs 24-27

M a t e r i a l e x a m i n e d : Switzerland: Holotype: Schwyz: SZ-3, 5 paratypes from the same sample. Holotype and 3 paraypes: MHNG, 2 paratypes (1611-PO-98): NHMH.

D i a g n o s i s : Rostral apex divided by two incisions, median apex triangular. Prodorsum with costulae and other structures. Sensilli narrow, fusiform with lateral branches. Anterior margin of notogaster straight, with lateral protuberances. Ten pairs of notogastral setae, setae c_2 long. Five pairs of genital setae, anogenital region normal.

M e a s u r e m e n t s : Length of body: 250-259 µm, width of body: 99-105 µm.

P r o d o r s u m : Rostrum divided by two small, but wide, U-shaped incisions, median apex triangular, also small (Fig. 24). Median costulae Y-shaped, weakly developed. Behind them, in the interbothridial position, one pair of elongated, nearly guttiform tubercles. Along the lamellar costulae, at their outer side, a pair of opposed smaller tubercles present on each side. Bothridia with posterior tubercles. The whole surface of prodorsum distinctly granulated or pustulated, also in the lamellar region (Fig. 27). All four pairs of prodorsal setae long, interlamellar ones thicker and more heavily ciliated than the others. Ratio among them: $in > ro \approx ex > le$. Sensilli very long, slightly dilated medially, bearing 5-6 lateral branches of different lengths on their distal parts.



FIGS 24-27

Oppiella besucheti sp. n. – 24: body in dorsal view, 25: body in ventral view, 26: podosoma in lateral view, 27: basal part of prodorsum.

L a t e r a l p a r t o f p o d o s o m a : Well sclerotized, nearly the whole surface well granulated and/or pustulated. Some longitudinal crests also present. Ventral border especially waved and incised, acetabula I-IV arranged nearly in one longitudinal line (Fig. 26). A pair of porose areae behind the bothridia clearly seen.

N o t o g a s t e r (Fig. 24): With one pair of granulate humeral apophyses. Dorsosejugal suture straight. Ten pairs of notogastral setae present, setae c_2 shorter than *la*, *lm* and *lp* also shorter than c_2, but nearly equal in length with the other setae, excepting p_2 and p_3. Setae h_1 characteristically directed outwards. Setae c_2 with cilia, all the other setae smooth.

V e n t r a l s i d e (Fig. 25): Well sclerotized, all apodemes and borders - excepting a part of the sternal ones - between the 2nd and sejugal apodemes well developed. Lateral margin of epimeres 1 framed by longitudinal borders bearing setae *1c*. A pair of inner costulae, parallel with discidium also present on epimeres 4 continued as undulate transversal parts. Setae *4b* arising on their posterolateral corner. Among the epimeral setae, setae *1c*, *3c*, but primarily and firstly setae *4c*, with long cilia. All other epimeral setae simple and smooth. Anogenital setal formula: 5 - 1 - 2 - 3. All setae simple. Lyrifissures *iad* long, placed in paraanal position.

L e g s : Setae of trochanters of legs II well arched, with conspicuously long cilia. Setae *p* of all tarsi simple, setiform. Solenidium φ of leg IV, very long, arched, longer than the joint.

R e m a r k s : See after the following species.

D e r i v a t i o n o m i n i s : I dedicate the new species to Dr. C. Besuchet (Muséum d'histoire naturelle, Geneva), the collector of the specimens and most of those soil samples from Switzerland which we studied recently in Geneva.

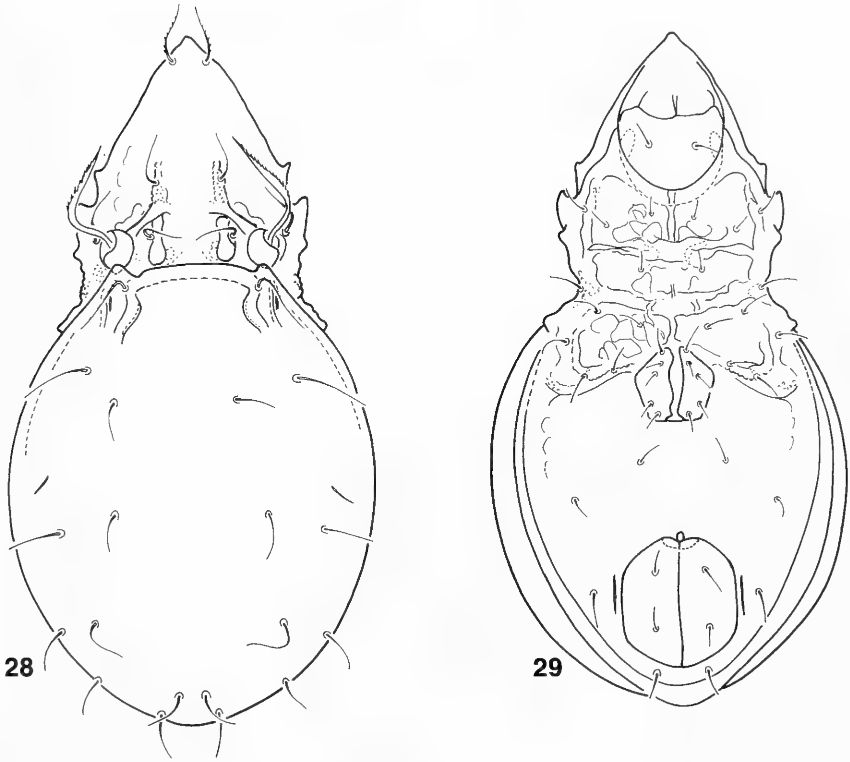
Oppiella propinqua sp. n. Figs 28-32

M a t e r i a l e x a m i n e d : Switzerland: Holotype: Luzern: LU-1 15 paratypes from the same sample. Holotype and 10 paratypes: MHNG, 5 paratypes (1612-PO-98): NHMH.

D i a g n o s i s : Rostrum nasiform. Lamellar costulae directed to the bothridia, one pair of basal protuberances present. Sensilli slightly fusiform, narrow, bearing short spines. Anterior margin of the notogaster straight, with well developed lateral protuberances. Ten pairs of notogastral setae, setae c_2 long. Anogenital region typical for the genus. Five pairs of genital setae.

M e a s u r e m e n t s : Length of body: 263-270 μm, width of body: 140-145 μm.

P r o d o r s u m : Rostrum slightly elongated, with a nasiform median apex. Lamellar costula well sclerotized, covered by pustules on their anterior part. A much finer transversal costula between them (sometimes it is hardly observable) (Fig. 30). A pair of elongated, guttiform tubercles in the interbothridial region bearing interlamellar setae on their outer margin and a pair of short laths at an angle between costulae and bothridia. Some weak sigillae visible laterally. Bothridia well developed, with a basal tubercle with a granulated field around it. Rostral setae characteristically arched inwards, ciliate. Lamellar setae arising on the distal half of the costulae. The



FIGS 28-29

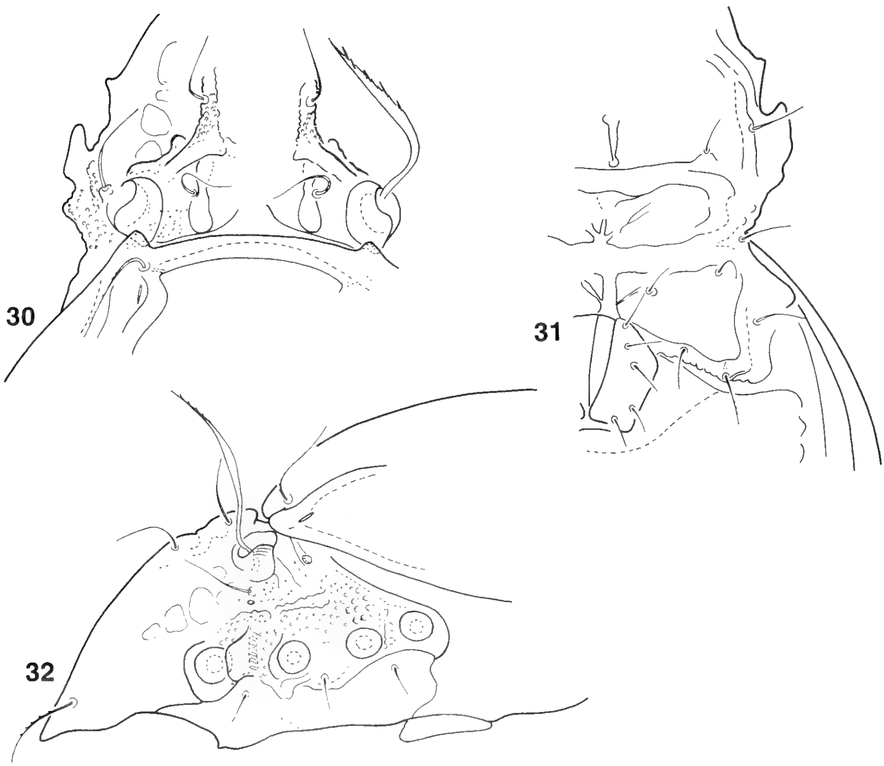
Oppiella propinqua sp. n. – 28: body in dorsal view, 29: body in ventral view.

ratio of the prodorsal setae: *ro* > *in* ≈ *ex* > *le*. Sensilli very long, their heads slightly dilated medially bearing some (5-7) very short spines.

L a t e r a l p a r t o f p o d o s o m a (Fig. 32): Well sclerotized, nearly the whole surface well granulated and/or pustulated. Some longitudinal crests also present. Ventral border, especially, undulate and incised acetabula I-IV arranged in one longitudinal line. A pair of indistinct porose areas behind the bothridia.

N o t o g a s t e r (Fig. 28): With one pair of large humeral apophyses. Dorsosejugal suture straight medially, slightly arched laterally, near the humeral tubercles. Ten pairs of notogastral setae present, setae c_2 and *la* equal in length, *lm* and *lp* much shorter than the preceding ones. Setae h_1 characteristically directed outwards, no essential difference among setae *h* and setae p_1. Setae c_2 with short cilia, all other setae smooth.

V e n t r a l s i d e (Fig. 29): Well sclerotized, all apodemes and borders - excepting a part of the sternal ones - between the 2nd and sejugal apodemes well developed. Lateral margin of epimeres 1 framed by longitudinal borders bearing



FIGS 30-32

Oppiella propinqua sp. n. – 30: basal part of prodorsum, 31: epimeral region, 32: podosoma in lateral view.

setae *1c*. A pair of inner costulae, parallel with the discidium also present on epimeres 4 continued as undulate transversal parts (Fig. 31). Setae *4b* arising on their posterolateral corner. All epimeral setae simple and smooth. Anogenital setal formula: 5 - 1 - 2 - 3. All setae simple. Lyrifissures *iad* long, located in paraanal position.

L e g s : Setae p of legs II - IV thick, clearly spiniform. Solenidium of tibia IV not longer than the joint.

R e m a r k s : *Oppiella nova* (Oudemans, 1902) is one of the most variable species of the genus *Oppiella* Jacot, 1937, however, it was designated as the type of the genus. Most authors consider this species as cosmopolitan, but nobody has made a comparative study on world material. Our opinion is, that this species comprises a number of closely related species. This opinion is strengthened in that some authors consider *Oppiella uliginosa* (Willmann, 1919) as a synonym of *O. nova* (e.g. Subías & Balogh, 1989). On the other hand Woas (1986) in his redescription of *O. uliginosa* quite obviously represents another species. The description and the drawings (Woas, 1986: 208, Abb. 102-103) surely do not refer to *O. nova*.

The two preceding new species stand very near to the type species of this genus, and e.g. *Oppiella primorica* (Golosova, 1970), which also belongs to this group. I also regard this genus as rather heterogeneous needing further study to demarcate its generic limits. Obviously, on the basis of the *O. nova* type, the diagnosis of the genus *Oppiella* should be complemented and restricted so that only those species which display the following characteristics should be included: Dorsosejugal margin with lateral apophyses. Among the epimeres, epimeres 1 framed laterally with a longitudinal border bearing setae *1c*, epimeres 4 framed posteriorly by an undulate (denticulate) lath, continuing anteriorly as a longitudinal inner costula. Other features should be investigated in the future.

Among the new species, on the basis of the undivided rostrum, *Oppiella propinqua* sp. n. stands closer to *Oppiella nova*. It is distinguishable from the type species by the form of the sensillus, which is longer in the new species. The other differential characters are: form of the prodorsal costula, the form and ratio of prodorsal setae, length and ciliation of epimeral setae (*1c*, *3c* and *4c*). The other species (*Oppiella besucheti* sp. n.) stands nearest to *Oppiella primorica* (Golosova, 1970) on the basis of the divided rostral apex (see also Mahunka, 1979). The new species is distinguishable from *Oppiella primorica* by the much larger median prodorsal apex and the thicker and ciliated interlamellar setae and the much wider basal guttiform tubercles in the interbothridial region in the new species.

Derivatio nominis: The new species belongs to the *Oppiella nova* species group.

Oxyoppioides decipiens (Paoli, 1908) Figs 33-37

Oppia decipiens Paoli, 1908: 69, figs 29, 48.
Oppia decipiens: Pérez-Iñigo, 1971: 297, fig. 30.
Oxyoppioides decipiens: Subías & Mínguez, 1985: 182.

Material examined: Switzerland: GE-4.

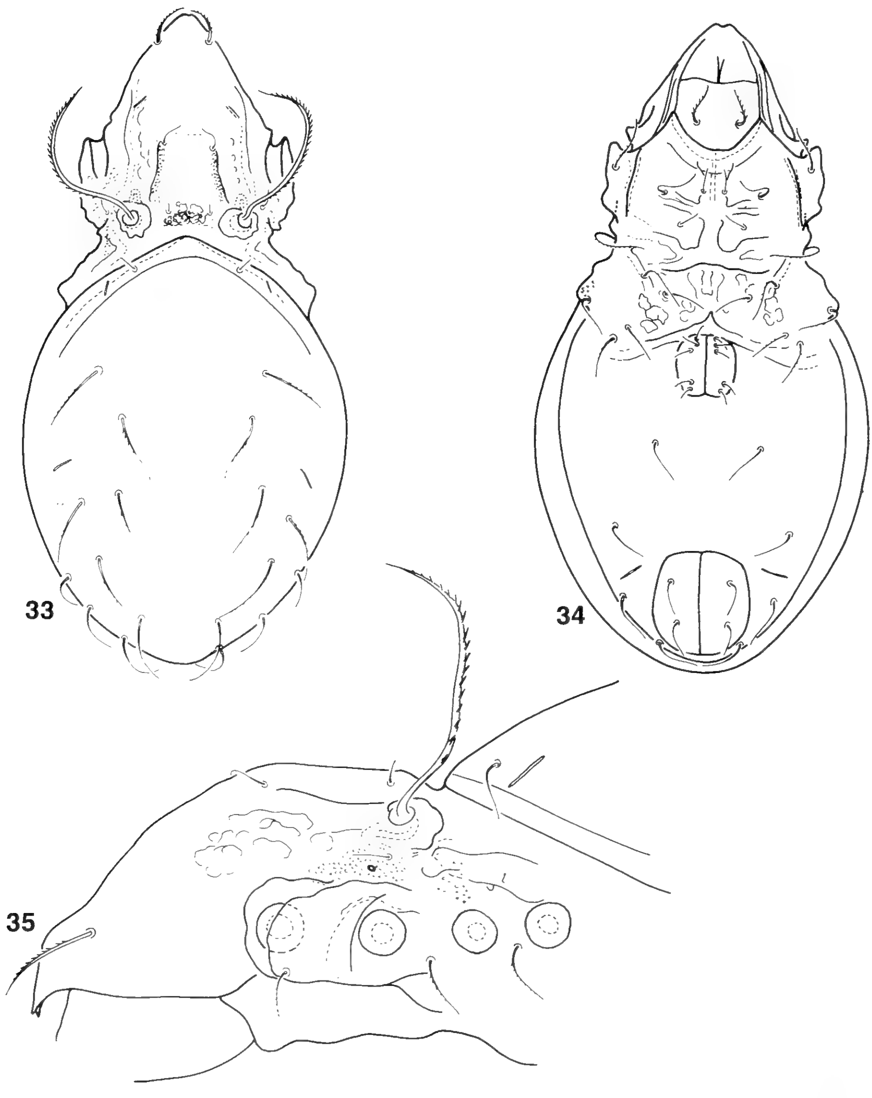
Remarks: The species has been collected several times in Central Europe, although it is more common in the Mediterraenean area. Several authors (e.g. Pérez-Iñigo, 1965; Subías & Mínguez, 1985) discussed it but no detailed redescription has been made. Furthermore,there are no available figures illustrating its leg structure. The following remarks complement our knowledge of this species.

Prodorsum: Rostrum U-shaped, excavated with two small, lateral teeth (Fig. 33). Costulae weak, surface densely granulate. Interbothridial region with numerous indistinct sigilla.

Lateral part of podosoma (Fig. 35): Weakly sclerotized, exobothridial region with fine granulation, with only poorly developed, longitudinal laths. Exobothridial setae short.

Notogaster: Humeral processes in the dorsosejugal region, hitherto characteristic for the genus *Oxyoppia*, entirely missing. Anterior margin of notogaster arcuate, closed in the middle.

Ventral side (Fig. 34): Apodemes very poorly developed. Epimeral borders hardly discernible in places. From among the sejugal and apodemes 4 and



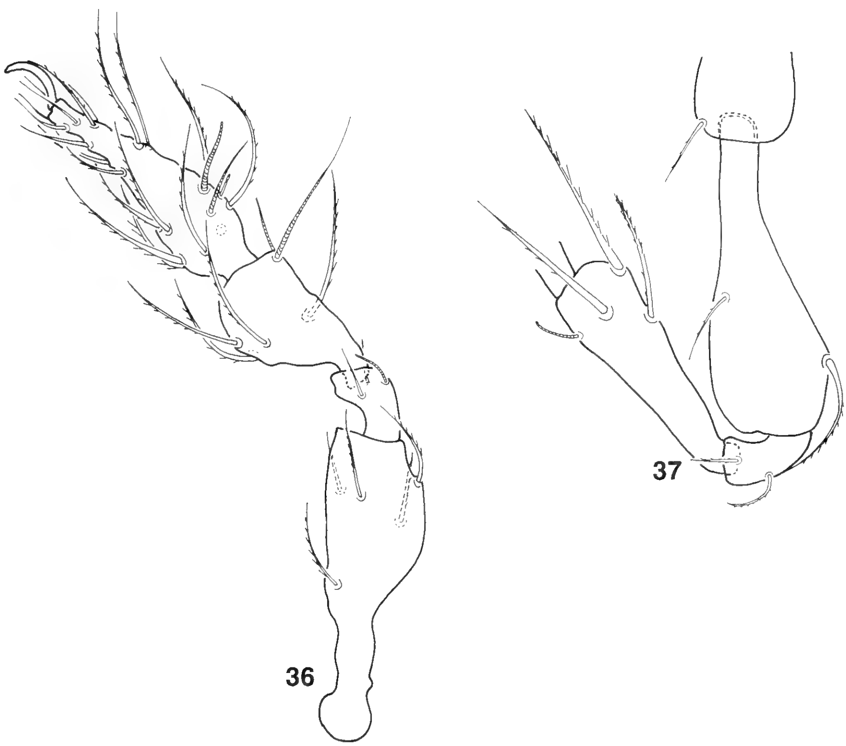
FIGS 33-35

Oxyoppioides decipiens (Paoli, 1908) – 33: body in dorsal view, 34: body in ventral view, 35: podosoma in lateral view.

borders the sternal apodeme and border are entirely missing. Surface of discidium granulate. Setae *1c* arising on pedotecta 1. Epimeral setae ciliate, setae *4a* and *4b* located strikingly close to each other. Anogenital formula 5-1-2-3. Aggenital setae arising one behind the other. Lyrifissure *iad* in inverse apoanal position, far removed from anal opening.

L e g s : Normal, oppioid type, only the tibia of leg I slightly thickened and the distal part of femur triangular (Fig. 36), solenidium of tibia of leg IV (Fig. 37) conspicuously short, and all setae characteristically long.

T a x o n o m i c p o s i t i o n : Subías & Balogh (1989) placed the genus in relationship with *Oxyoppia*. We do not agree with this opinion, although the genus is soundly based. The key published by them is unsuitable for its identification. The position of lyrifissure *iad*, said to be paraanal, is also in error in the key of Balogh & Balogh (1992).



FIGS 36-37
Oxyopioides decipiens (Paoli, 1908) – 36: leg I, 37: femur, genu and tibia of leg IV.

Paramedioppia gen. n.

D i a g n o s i s : Family *Oppidae*. Rostrum divided by two incisions. Weak costulae with a transcostula and one pair of interbothridial "tubercles" present on prodorsum. Sensilli setiform, with some irregular spines. Dorsosejugal part of notogaster gradually arched, not penetrating into the interbothridial region. Crista present, setae c_2 arising medially. Ten pairs of notogastral setae present. Among the epimeral

setae *1c* arising on the epimeral surface, epimeral borders and apodeme normally developed. Anogenital setal formula 6 - 1 - 2 - 3. Lyrifissures *iad* in paraanal position. Gnathosoma, chelicerae and palps normal. Legs very long, joints of leg IV especially elongated.

Type species: *Paramedioppia helvetica* sp. n.

Remarks: The new taxon seems to be a mixture of two genera: *Oppiella* Jacot, 1937 and *Medioppia* Subías & Mínguez, 1985. The latter is a highly heterogeneous genus, as is *Oppiella*. The type species of the genus *Medioppia*, *O. media* Mihelcic, 1956 (Pérez-Iñigo, 1965) does not have costulae but has interbothridial tubercles. On the other hand, it has 5 pairs of genital setae, and its rostrum is undivided. Thus, we could not relegate the new species into any of the known genera.

Derivatio nominis: Similar to the genus *Medioppia*.

Paramedioppia helvetica sp. n. Figs 38-42

Material examined: Switzerland: Holotype: Tessin: TI-9, 1 paratype from same sample. Holotype: MHNG, paratype (1616-PO-98): NHMH.

Diagnosis: Rostrum divided, rostral apex truncate. Prodorsum weakly sclerotized, short longitudinal and transversal costulae present. Sensilli setiform with irregular spines. Anterior margin of notogaster convex. Cristae present. Ten pairs of notogastral setae, setae c_2 long. Anogenital setae normal, six pairs of genital setae.

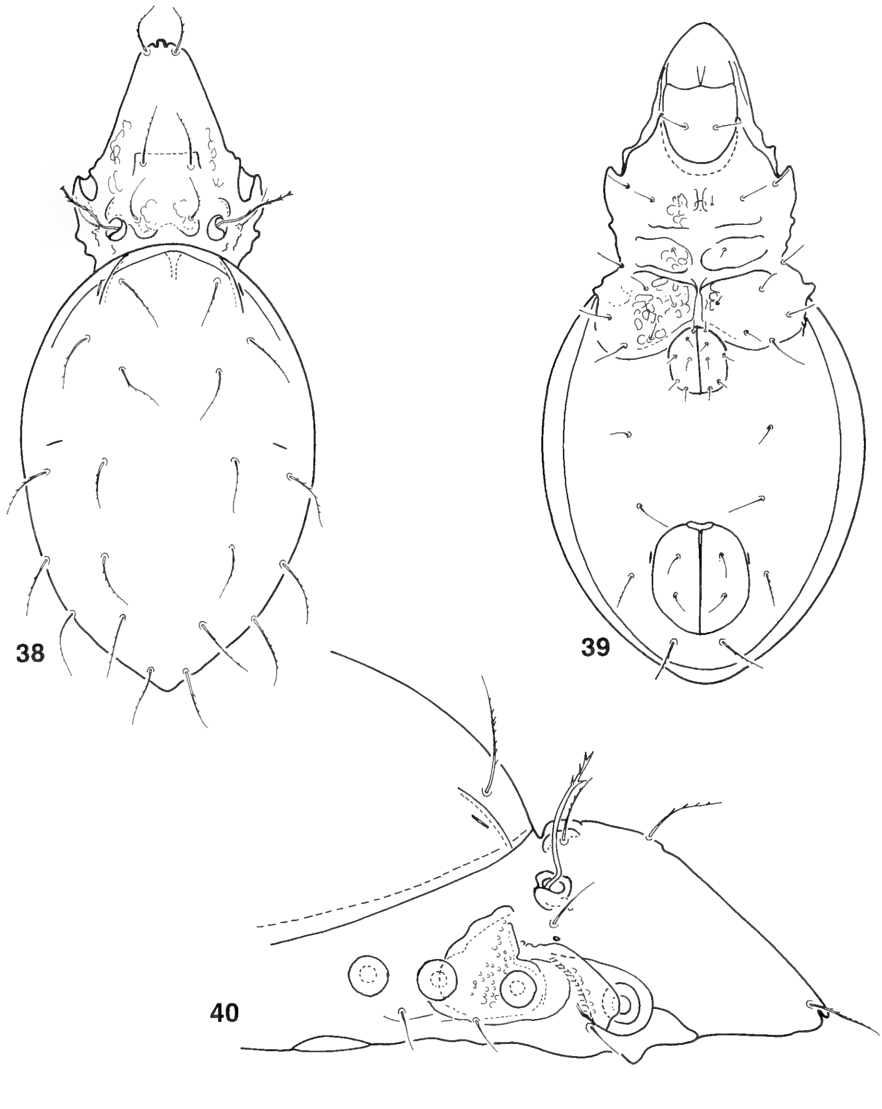
Measurements: Length of body: 762-823 µm, width of body: 369-403 µm.

Prodorsum: Elongated. Rostral part rounded, but flanked by two short incisions. Median apex truncate, lateral apices rounded. Prodorsal surface weakly sclerotized, but short longitudinal costulae with distinct corners, a very weak transcostula and a pair of interbothridial, arched tubercles present. Some indistinct sigilla also observable. Bothridia without posterior tubercles. Rostral setae arising on the prodorsal surface, lamellar setae located behind the costular corners (Fig. 38). Ratio of prodorsal setae: : $in \approx ro > le > ex$. Sensilli well characteristic for the species, bent several times, setiform, with 4-5 spines, without capitula, their distal ends simple or bifurcate.

Lateral part of podosoma: Pedotecta 1 comparatively well developed. Exobothridial surface not granulate, some granules observable betweeen the acetabula II - III. This part well framed by a lath, above the acetabula (Fig. 40).

Notogaster: Conspicuously elongated. Crista weak, but distinct also a pair of short and weak median lines present at the dorsosejugal margin of the notogaster (Figs. 38, 40). Ten pairs of notogastral setae of equal length present, all ciliate.

Ventral side (Fig. 39): Apodemes and borders weakly developed. Marginal, longitudinal lath absent on epimera 1. In anteromedian sternal apodemes a ring-like feature present on the sternal apodemes, between setae *1a*. All epimeral setae simple, thin, setiform. Epimeral surface ornamented by polygonal pattern. Six pairs of genital setae arising in two rows (4 pairs in median, 2 pairs in lateral position). Adanal setae ciliate, like the notogastral ones, other setae in the anogenital region simple.

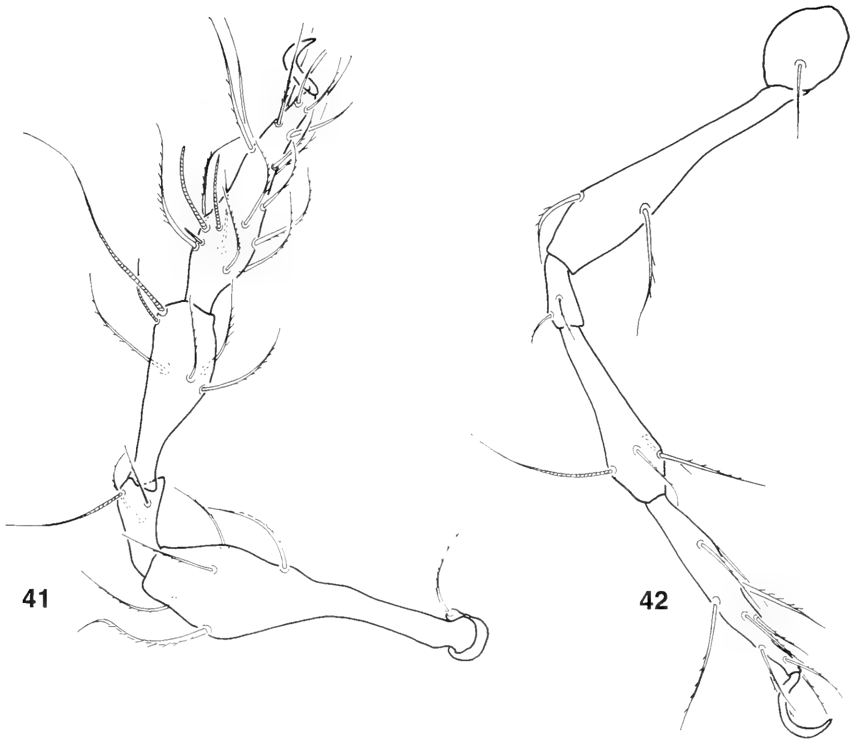


FIGS 38-40

Paramedioppia helvetica gen. n., sp. n. – 38: body in dorsal view, 39: body in ventral view, 40: podosoma in lateral view.

L e g s : All joints long, not widened, setae conspicuously ciliate/spinose. Leg setal formulae are normal for the family:

I: 1 - 5 - 2+1 - 4+2 - 20+2 - 1 (Fig. 41)
IV: 1 - 2 - 2 - 3 +1 - 10 - 1 (Fig. 42)



FIGS 41-42

Paramedioppia helvetica gen. n., sp. n. –41: leg I, 42: leg IV.

R e m a r k s : The main features are mentioned in the generic diagnosis, but it is the form of the sensillus which well characterises the new species.

D e r i v a t i o n o m i n i s : Named after the country the species originates from.

Subiasella (Lalmoppia) quadrimaculata (Evans, 1952)

Oppia quadrimaculata Evans, 1952: 37, fig. 2.
Subiasella (*Lalmoppia*) *quadrimaculata*: Subías & Rodriguez, 1986: 114, figs 1-3.

M a t e r i a l e x a m i n e d : Switzerland: GR-10.

R e m a r k s : The species is known from several localities (from England to Poland) of Europe, but it is not frequent anywhere. This is its first record from Switzerland. The prodorsum of these specimens, as it is the case in the Hungarian ones, has neither costula nor lamellar line.

Quadroppiidae Balogh, 1983

There is a great confusion in the family Quadroppiidae partly due to the publication of Mínguez et al. (1985) and partly to Woas (1986) but specifically to that of the latter author who synonymized species without the study of types. The core of the problem is in the interpretation of the senior author's species (*Quadroppia michaeli* Mahunka, 1977) described from Greece, and on the other hand, Woas' interpretation of the type species, *Q. quadricarinata* (Michael, 1885[3]) which was misunderstood by Paoli (1908). Accordingly, if the *Q. michaeli* species is not new, but simply the misinterpreted *Q. quadricarinata*, then the name introduced by Woas as *Q. paolii* nom. n. is redundant.

The situation is further aggravated in that the senior author described with Paoletti (Mahunka & Paoletti, 1984) another new species belonging to this genus (*Q. omodeoi* Mahunka & Paoletti, 1984), without taking the trouble to point out its relationship with the *Q. quadricarinata* by then correctly understood. Our recent study has revealed that *Q. paolii* is probably identical with the specimens from Switzerland, and we further believe that it is not identical either with *Q. quadricarinata* sensu Mahunka, nor with the form interpreted by Paoli, nor *Q. omodeoi*. There is a further problem in that Mínguez *et al.* (1985) hold the view that Hammer's *Q. monstruosa* is the same of Paoli's *Q. quadricarinta*.

To clarify the problem thorough study of types is needed along with authentically identified specimens. This time we could only examine the types of *Q. michaeli* and *Q. omodeoi*, and those Greek specimens which were published in 1977 as *Q. quadricarinata* sensu Mahunka. We discuss *Q. longisetosa* Mínguez, Ruiz et Subías, 1985 that was also found in Switzerland (*Q. quadricarinata* (Michael, 1885) was also collected at several localities in Switzerland) but refrain from discussing the other species here.

Quadroppia longisetosa Mínguez, Ruiz & Subías, 1985 Figs 43-44

Quadroppia longisetosa Mínguez *et al.*, 1985: 104, figs 6-7.

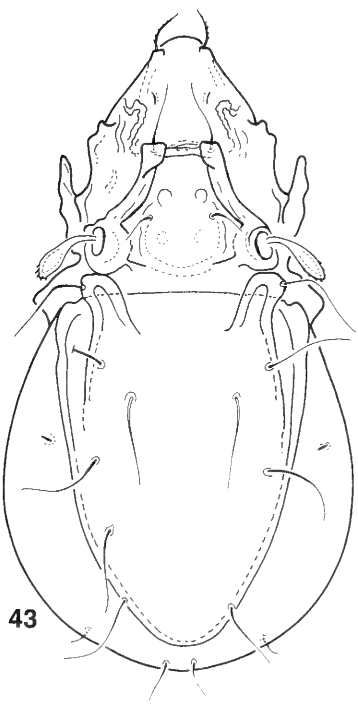
Material examined: Switzerland: NW-1.

Remarks: This species is readily identifiable among the members of the genus *Quadroppia* Jacot, 1939. The Swiss specimens correspond well with the description and the figures of the species. Some slight differences exist, like the weak longitudinal lath in the interlamellar region parallel with the costulae, and the notogastral setae are somewhat more rigid than depicted in the drawing. We provide some figures obtained from specimens taken in Switzerland .

Quadroppia michaeli Mahunka, 1977 Fig. 45

Quadroppia michaeli Mahunka, 1977: 914, Abb. 12.
Quadroppia michaeli: Mínguez *et al.*, 1985: 114, figs 17-18.
Quadroppia michaeli: Mahunka, 1977 sensu Woas, 1986: 215.

[3] The original description appeared in 1885 and not in 1887 as mentioned by Woas (1986).



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FIGS 43-44

Quadroppia longisetosa Mínguez, Ruiz & Subías, 1985 – 43: body in dorsal view, 44: body in ventral view.

Remarks: In spite of Woas' opinion, this is a valid, independent species. It cannot be brought into close relationship with any of the so far described species. Its characteristics are:

Prodorsum: Oval crest in the rostral region undivided and gradually becoming narrower basally. On both sides an arcuate, well separated crest present. Intercostular region with a short, transverse lath directly behind the distal end of costulae.

Notogaster: The posteriorly running ribs emanating from the humeral processes are not weaker than the ones beside them, length of ribs is the same.

Ventral side: Epimeral borders are shown in Fig. 45. The median pattern directly in front of the genital opening is highly characteristic, it comprises two touching parts, both are rounded.

Legs: Tarsus of leg II bears 2 solenidia.

Quadroppia omodeoi Mahunka & Paoletti, 1984 Figs 46-47

Quadroppia omodeoi Mahunka & Paoletti, 1984: 114, figs 1-2.

R e m a r k s : All the known species are distant relatives only. Its characteristics are:

P r o d o r s u m : Oval crest in the rostral region is undivided, not strongly narrowing basally. Intercostular region with a short, concave, transverse lath directly behind the distal end of costulae. Behind this transverse lath 2 pairs of sigillae and one pair of lateral laths are present, the latter are not connected in the middle. Sensilli conspicuously long (Fig. 47), much longer than in the other species.

N o t o g a s t e r : The posteriorly running ribs emanating from the humeral processes are much longer than the lateral ones. Notogaster completely enframed by a rib.

V e n t r a l s i d e : Fig. 46 depicts the epimeral borders.

L e g s : Tarsus of leg II bears 2 solenidia.

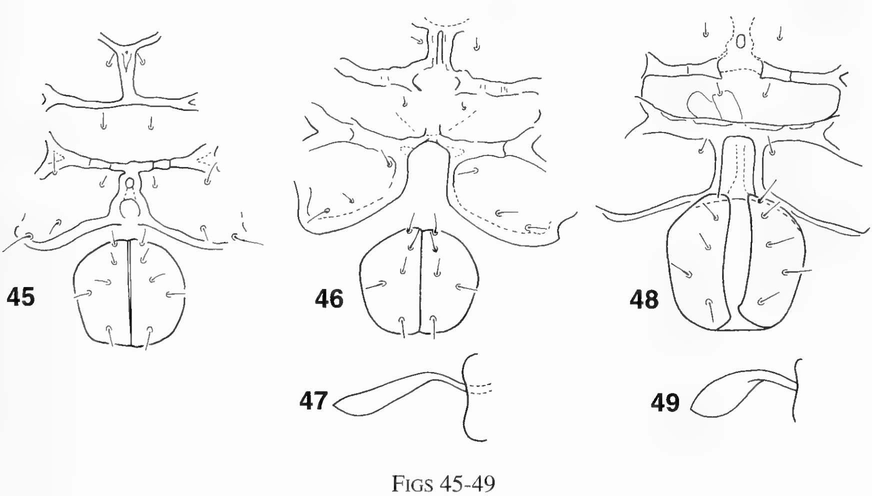
Quadroppia* cf. *paolii Woas, 1986 Fig. 48-49

Quadroppia paolii Woas, 1986: 78, figs 30-32.

M a t e r i a l e x a m i n e d : Switzerland: GR-10.

R e m a r k s : Without studying the type the relegation of this species is impossible. It is highly probable that this species may be identical with *Q. monstruosa* Hammer, 1979 sensu Mínguez *et al.* (1985). Fundamental differences are obvious:

P r o d o r s u m : Oval crest in the rostral region is either entirely divided basally or much variegated. Intercostular region with a long, robust, arcuate lath directly before the end of costulae. Just behind this 2 pairs of sigillae and one pair of lateral laths, the latter frequently connected in the middle with a weak, transverse lath. Sensillar capitula oval (Fig. 49).



Figs 45-49

Quadroppia michaeli Mahunka, 1977 – 45: epimeral region.
Quadroppia omodeoi Mahunka & Paoletti, 1983 – 46: epimeral region, 47: sensillus.
Quadroppia cf. *paolii* Woas, 1986 – 48: epimeral region, 49: sensillus.

Notogaster: The posteriorly running ribs emanating from the humeral processes are shorter than the lateral ones.

Ventral side: as shown in Fig. 48.

Legs: Tarsus of Leg II bearing 2 solenidia.

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Rudolphiella szidati sp. n. (Proteocephalidea: Monticelliidae, Rudolphiellinae) parasite of *Luciopimelodus pati* (Valenciennes, 1840) (Pisces: Pimelodidae) from Argentina with new observations on *Rudolphiella lobosa* (Riggenbach, 1895)

Alicia A. GIL DE PERTIERRA[1] & Alain de CHAMBRIER[2]

[1] Departamento de Ciencias Biológicas, Lab. 52, Facultad de Ciencias Exactas y Naturales, Pab. II, Ciudad Universitaria, U.B.A., 1428 - Buenos Aires, Argentina. e-mail: helminto@bg.fcen.uba.ar

[2] Département des Invertébrés, Muséum d'histoire naturelle, PO Box 6434, CH -1211 Geneva 6, Switzerland. e-mail: alain.dechambrier@mhn.ville-ge.ch

Rudolphiella szidati sp. n. (Proteocephalidea: Monticelliidae, Rudolphiellinae) parasite of *Luciopimelodus pati* (Valenciennes, 1840) (Pisces: Pimelodidae) from Argentina with new observations on *Rudolphiella lobosa* (Riggenbach, 1895). - *Rudolphiella szidati* sp. n. (Cestoda, Monticelliidae, Rudolphiellinae) is described from the anterior intestine of the pimelodid fish, *Luciopimelodus pati* caught in Paraná river and de la Plata river (Argentina). Additional informations to the description of the type material of *Rudolphiella lobosa* (type species of the genus) is given. *R. lobosa* was not found in *L. pati* (as reported originally by Riggenbach, 1895) and has never been found since its original description. The new species differs from other species of *Rudolphiella* by its larger scolex, a higher number of testes and by its distinct egg shape. A diagnosis of *Rudolphiella* is given. The following taxonomical actions are introduced: *Rudolphiella piracatinga* (Woodland, 1935) comb. nov. for Monticellia piracatinga Woodland, 1935; *Monticellia rugata* Rego, 1975 syn. nov. of *Rudolphiella piracatinga* (Woodland, 1935). The presence of glandular cells within the scolex's apex is observed in all known *Rudolphiella* species i.e. *R. lobosa*, *R. myoides*, *R. szidati*, *R. piracatinga*, *R. piranabu*. *Rudolphiella*, the sole genus within Rudolphiellinae, is widespread in a monophyletic group of hosts (*Calophysus*-group sensu de Pinna, 1998) suggesting likely coevolution.

Key-words: Proteocephalidea – Monticelliidae – *Rudolphiella szidati* sp. n. – *Rudolphiella lobosa* – *Luciopimelodus pati* – coevolution – Argentina.

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INTRODUCTION

Riggenbach (1895) described *Corallobothrium lobosum* parasite of *Luciopimelodus pati* (Valenciennes, 1840) from Paraguay River, Paraguay. Later, Fuhrmann (1916) redescribed Riggenbach's material adding information of proglottides' transverse sections, and erected a new genus *Rudolphiella* Fuhrmann, 1916 to allocate *Corallobothrium lobosum* Riggenbach, 1895. This species has never been found since its original description.

Woodland (1934) erected the genus *Amphilaphorchis* and described two species *Amphilaphorchis piranabu* Woodland, 1934 and *A. myoides* Woodland, 1934, both parasites of *Pinirampus pirinampu* (Spix, 1829). A year later Woodland (1935), concluded that genus *Amphilaphorchis* Woodland, 1934 is a synonym of *Rudolphiella* and erected a new subfamily, the Rudolphiellinae.

The examination of *Luciopimelodus pati* (Valenciennes, 1840) from Paraná river and de la Plata river, Argentina, the type host of *R. lobosa* (Riggenbach, 1895) revealed the presence of a new species of *Rudolphiella* described herein. Since the original description of *Rudolphiella lobosa* (Riggenbach, 1895) did not contain data on some useful morphological structures, the type material of this species is restudied.

MATERIAL AND METHODS

Sixty-two specimens of *Luciopimelodus pati* (Valenciennes, 1840) were examined for helminths. Forty intestines were placed in lukewarm water in order to relax the worms and then fixed in AFA, while others were dissected and fixed directly in hot 4% formaldehyde solution and were subsequently stored in ethanol 75 % V/V. Entire tapeworms were stained with Langeron's alcoholic chlorhydric carmine (Langeron, 1949), differenciated in acid ethanol, dehydrated in ethanol, cleared in beechwood creosote or in eugenol, and mounted in Canada balsam. Thick transverse hand-cutting sections of the proglottides were stained following equivalent procedure. Two scolices and pieces of strobilas were embedded in paraffin, transversely sectioned at 12-15 µm, stained with Weigert´s hematoxylin and counterstained with 1% eosin B and mounted in Canada balsam. Eggs were mounted in distillated water for drawing. Two scolices were prepared for scanning electron microscopy (SEM), they were dehydrated through a gradual series of ethanol, then put in amyl acetate, critical point dried and sputtered with gold and photographed with a Zeiss DSM 940 A SEM.

Rudolphiella szidati sp. n. type material was deposited at the Helminthological Collection of the "Museo Argentino de Ciencias Naturales Bernardino Rivadavia", Buenos Aires, Argentina (MACN), and at the Natural History Museum, Geneva, Switzerland (MHNG). We also studied syntypes of *R. piranabu* (Woodland, 1934) BMNH 1964.12.15.101.107 and syntypes of *R. myoides* (Woodland, 1934) BMNH 1964.12.15.108.110, (Amaz 74.3), both parasites from *Pinirampus pirinampu* (Spix, 1829); syntypes of *R. piracatinga* (Woodland, 1935) BMNH 1964.12.15.206-208, (Amaz 40) from *Calophysus macropterus* (Lichtenstein, 1819) from the British Museum of Natural History, London (BMNH). Amaz = field numbers of Woodland's material.

All measurements are given in micrometres, unless otherwise stated, with the range followed by the mean (m) and the number of measurements (n) in parentheses. MT = type material. Illustrations were made with the aid of a camera lucida.

RESULTS

Rudolphiella Fuhrmann, 1916

Syn. *Amphilaphorchis* Woodland, 1934

Diagnosis: Proteocephalidea, Monticelliidae, Rudolphiellinae. Worms of small or medium size; wrinkle collar-like metascolex; suckers uniloculate with developed internal circular musculature in their distal margin; apical glandular cells arranged in a cross situated between the suckers and the apical tegument; internal longitudinal musculature developed; testes cortical in one layer; vagina posterior or anterior to cirrus pouch, when anterior ventrally overlapping the cirrus pouch; genital pores irregularly alternating; ovary medullar with outgrowths in cortex, strongly lobulate; vitelline follicles cortical, ventral, with a tendency of posterior concentration; uterine primordium and lateral branches medullar; eggs with elongated shell and with embryophores bearing two elongated polar projections; all species parasites of catfishes of the family Pimelodidae. Type species: *Rudolphiella lobosa* (Riggenbach,1895)

Rudolphiella szidati sp. n. Figs 1, 3-5, 8, 11

Host: *Luciopimelodus pati* (Valenciennes, 1840) (= *Pimelodus pati*), common name: patí.

Material studied: Argentina, Provincia de Corrientes, Ciudad de Corrientes, Puerto Italia (Paraná river), holotype MHNG: 26251 INVE, 30.07.1997, paratypes MHNG: 26252 - 26256 INVE, 30.07. to 01.08.1997; Argentina, Provincia de Chaco, Pte General Belgrano (Paraná river) (27° 27´S, 58° 50´W), 8 paratypes MACN: 392/1-8; Argentina, Provincia de Buenos Aires, Puerto de Buenos Aires (de la Plata river) (34° 37´S, 58° 22´W), MACN 392/9-10, 2 paratypes, 06.06.1995; other material: Argentina, Provincia de Corrientes, Ciudad de Corrientes, Puerto Italia (Paraná river), 24667 - 24674, 27235 INVE, 30-31.07.1997 and MACN 392/11-15.

Site of infection: anterior portion of intestine and rarely in first portion of medium intestine.

Prevalence: 100%, 62 fishes examined.

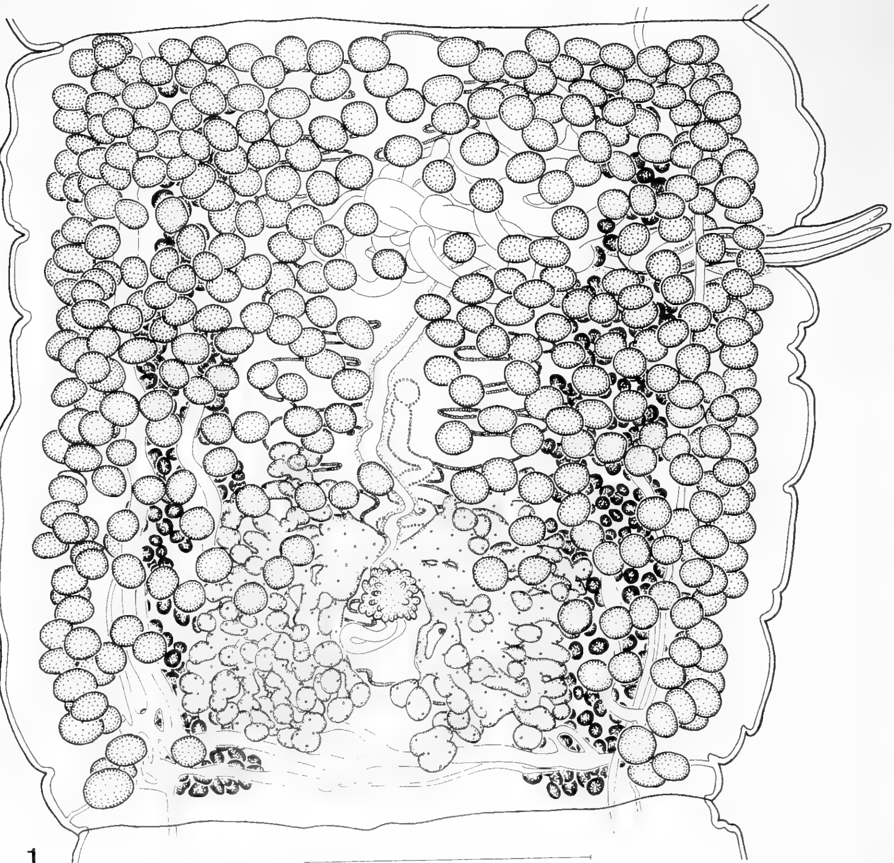
Intensity: 2-52; m = 20

Etymology: the new species honours Prof. Lothar Szidat (Buenos Aires).

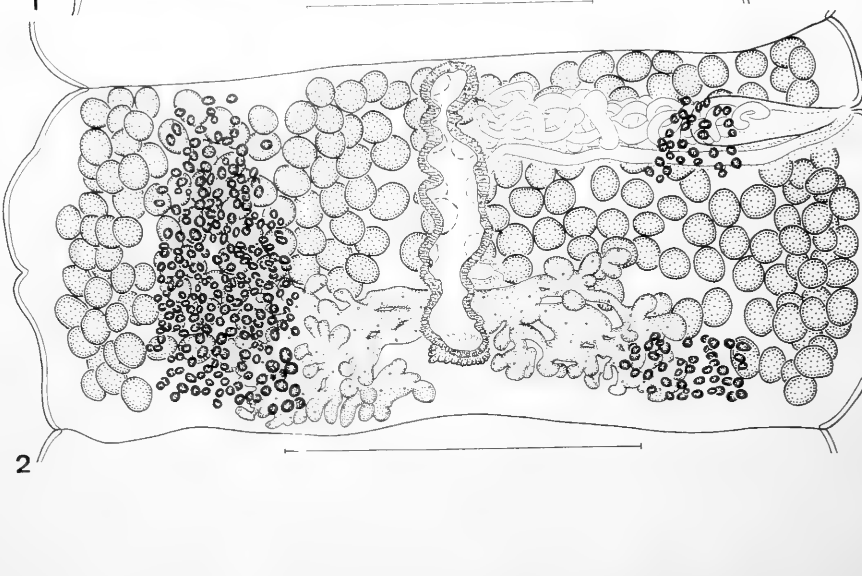
DESCRIPTION (based on 30 specimens and measurements on 8 specimens):

Monticelliidae, Rudolphielliinae. Testes cortical, situated dorsally and surrounding laterally and ventrally the longitudinal muscular bundles, reaching but not overlapping the vitelline follicles (Fig. 4); ovary medullar with projections into the cortical parenchyma (Fig. 5); uterus medullar (uterine stem and lateral branches). Vitelline follicles cortical in 2 ventral bands (Figs 1, 4-5).

Medium size worms, flattened dorso-ventrally, total length 16-27 mm (m = 22, n = 8). Strobila with wrinkles and furrows, acraspedote, comprising about 22-37 (m = 28, n = 8) proglottides, fast maturation (10-18 immature proglottides, 4-6 mature proglottides and 6-10 gravid proglottides).



1



2

Wrinkle collar-like metascolex (in the sense of de Chambrier & Paulino, 1997) (Fig. 11), encircling the anterior part of the scolex, 1735-2970 in diameter. Metascolex with apical elongated bottle-shape glandular cells with granular inclusions, arranged in a cross situated between the suckers and the apical tegument (Fig. 3a); 4 slightly oval uniloculate suckers. 395-595 (m = 490, n = 19) long and 345-560 (m = 415, n = 19) wide; presence of internal circular musculature on distal margin of suckers (Fig. 3b); suckers usually hidden by the collar-like metascolex. The suckers are visible when the scolex is fixed outside the gut.

Proliferation zone 990-2970 (m = 2005, n = 8) long, 625-1050 (m = 845, n = 8) wide. Immature proglottides 130-530 (m = 310, n = 26) long, 695-1485 (m = 1080, n = 26) wide; mature proglottides 380-1110 (m = 610, n = 34) long, 925-1780 (m = 1330, n = 34) wide. Gravid proglottides 495-1500 (m = 965, n = 37) long, 775-1895 (m = 1425, n = 37) wide. Last proglottis 2145 long, 990 wide.

Internal longitudinal musculature developed, forming a thick bundle of thin muscular fibres (Figs 4-5). Osmoregulatory canals thick-walled, with anastomoses in the last third of proglottis. Ventral canals interconnected posteriorly to ovary (Fig. 1). Ventral canals 20-45 in diameter and dorsal canals 8-30 in diameter. A thin lateral ventral secondary duct of ventral osmoregulatory canal opens on each posterior side of the proglottis, forming a vesicle before ending in the tegument. This structure was also observed in *R. lobosa* by Riggenbach (1896).

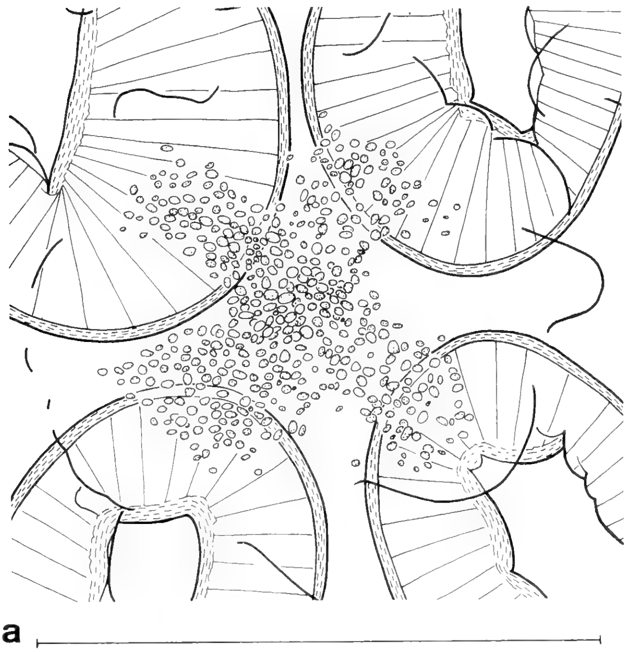
Testes spherical, 50-70 in diameter, 289-365 (m = 325, n = 6), one-layered, in a compact single field, located in the cortical parenchyma, dorsal, lateral and ventral in part, not interrupted at cirrus pouch level; overlapping the anterior margin of the ovary and laterally reaching the posterior end of the proglottis (Fig. 1).

Genital pores alternating irregularly, in 20-46% (m = 30%, n = 34) anterior of proglottis length. Ejaculatory duct coiled. Cirrus pouch thin-walled, 230-330 (m = 270, n = 34) long, 60-110 (m = 85, n = 34) wide. Cirrus pouch length occupying 15-32% (m = 23%, n = 34) of proglottis width. Vas deferens bulky and very coiled, sometimes reaching body midline, usually reaching anterior margin of mature proglottis, occupying aproximately one third of mature proglottis length (Fig. 1).

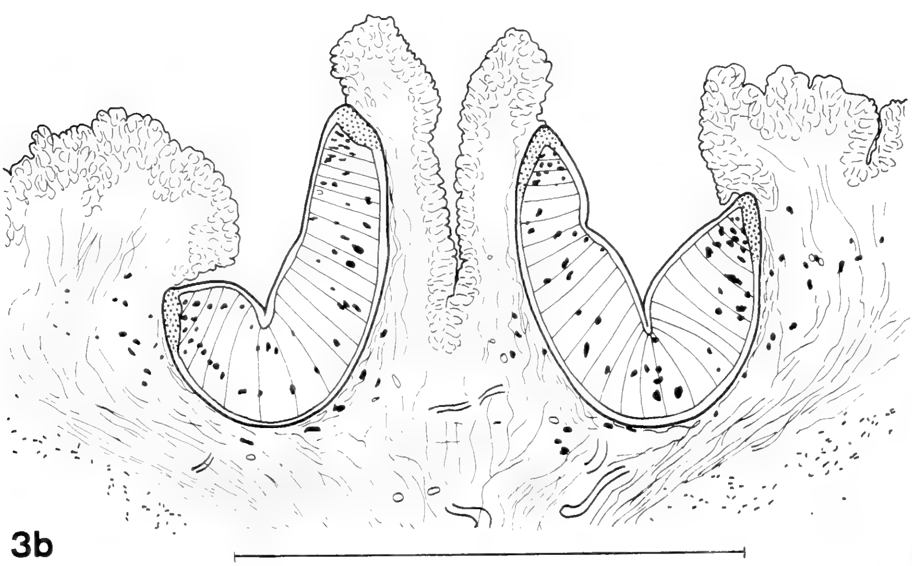
Vagina thick- walled, forming 1-2 loops near the ovary. Vagina posterior (77%) or anterior (23%) to cirrus pouch; when the vaginal duct is anterior, ventrally overlapping cirrus pouch, not surrounding the coiled vas deferens as is common. Ovary medullar, bilobed, strongly lobulate with dorsal and ventral outgrowths, only dorsal projections reach the cortex. Ovary occupying 43-68% (m = 53%, n = 34) of proglottis width (Fig. 1).

FIGS 1-2

1. *Rudolphiella szidati* sp. n., holotype 26251 INVE, pregravide proglottis, dorsal view. 2. *Rudolphiella lobosa* (Riggenbach, 1896), syntype-material, 43/43, pregravide proglottis, ventral view (coll. Zoological Institute, Neuchâtel). The vitelline follicles on the right side are not entirely represented. Scale-bar, 500 µm.

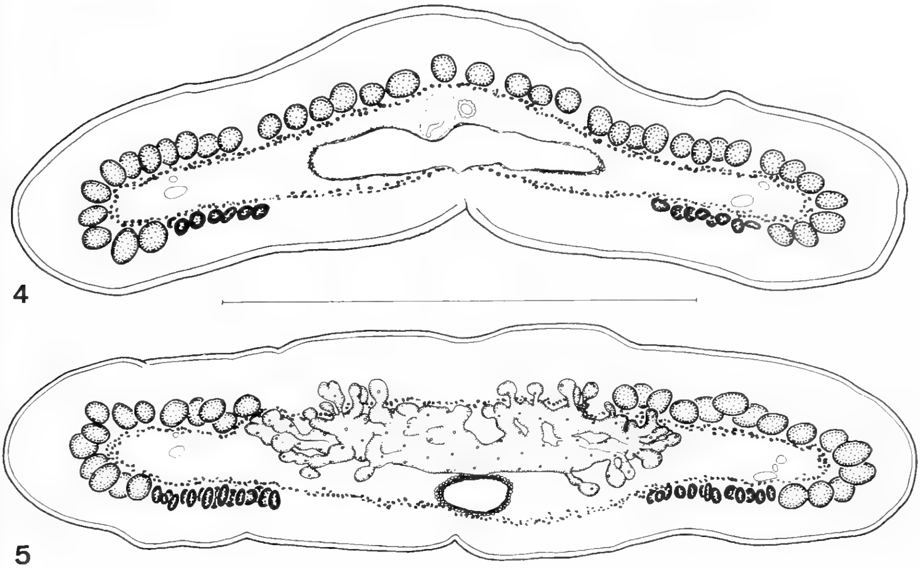


3a



3b

FIGS 3a-b. *Rudolphiella szidati* sp. n. 3a. 24673 INVE, apical view of scolex, detail of the apical portion showing the granular cells in a cross shape situated below the tegument. 3b. 27235 INVE, parasagittal section of scolex showing the internal circular musculature in their distal margin. Scale-bar, 500 µm.



FIGS 4-5

Rudolphiella szidati sp. n., paratype, 26253 INVE, transverses sections of a pregravide proglottis. 4. Sections at ovary level; 5. Sections at posterior part of proglottis. Scale-bar, 1000 μm.

Vitelline follicles cortical in 2 ventral bands, sometimes reaching anterior and posterior margin of proglottis, with a tendency to a posterior concentration of follicles, uninterrupted by cirrus pouch and vagina (Figs 1, 4-5).

Uterine primordium medullar originating from a cylindrical mass of chromophil cells. Lumen appearing in first mature proglottides. Medullar uterine branches up to 70% (m = 34%, n = 37) of gravid proglottis width, with 9-17 lateral branches opposite to cirrus pouch and 7-16 on cirrus pouch side.

Eggs with elongated polar projections aproximately of equal size (Fig. 8); thin, hyaline and spindle-drop shaped external shell. Outer envelope 128-167 (m = 140, n = 12) long, 20-23 (m = 21, n = 12) wide. Inner envelope consisting in bilayered embryophore, with nucleate envelope 16-21 (m = 20, n = 12) long, 10-16 (m = 14, n = 12) wide and external layer 40-50 (m = 45, n = 12) long, 18-21 (m = 20, n = 12). Oncosphere slightly oval, 10-13 (m = 11, n = 12) long, 7-13 (m = 10, n = 12) wide; oncosphere hooks, 3-6 (m = 4, n = 17); According to Swiderski (1994), we interprete the described structures as: 1. Shell; 2. Outer envelope; 3. Inner envelope consisting in bilayered embryophore with external layer much bigger than nucleate envelope; 4. Oncospherical membrane rarely visible; 5. Oncosphere.

Rudolphiella lobosa (Riggenbach, 1895) Fuhrmann, 1916 Fig. 2

syn. *Corallobothrium lobosum* Riggenbach, 1895; *Ephedrocephalus lobosum* (Riggenbach,1895) Mola, 1906.

Host (according to Riggenbach, 1895): *Pimelodus pati* (= *Luciopimelodus pati* (Valenciennes, 1840), common name: patí.

Material examined: Paraguay, Paraguay river, type-material, slides 43/43-44 (Collection of the Institute of Zoology, Neuchâtel, deposited in the MHNG), collected by Ternetz, 01-02.1894.

Site of infection: intestine.

DESCRIPTION:

Strobila acraspedote, with wrinkles and furrows; worms of medium size 17-22 mm long, with fast maturation. Scolex with apical glandular cells arranged in a cross, situated between the suckers and the apical tegument, presence of a well developed metascolex, 1025-1350 wide. Suckers uniloculate 205-245 in diameter, with free distal muscular sphincter. Proliferation zone about 800 long. Longitudinal muscular fibers developed all around the proglottis.

Testes in one layer in transverse sections, in a single field, sphaerical 50-65 in diameter, 194-219 (m = 206; n = 3) (53 in original figure of Riggenbach (1896), 150-200 according to Riggenbach (1896), 220 according to Fuhrmann (1916)) in number. Testes in cortical parenchyma, dorsal, lateral and ventral in part, not interrupted at cirrus pouch level; overlapping anterior margin of ovary and laterally reaching posterior end of the proglottis (Fig. 2).

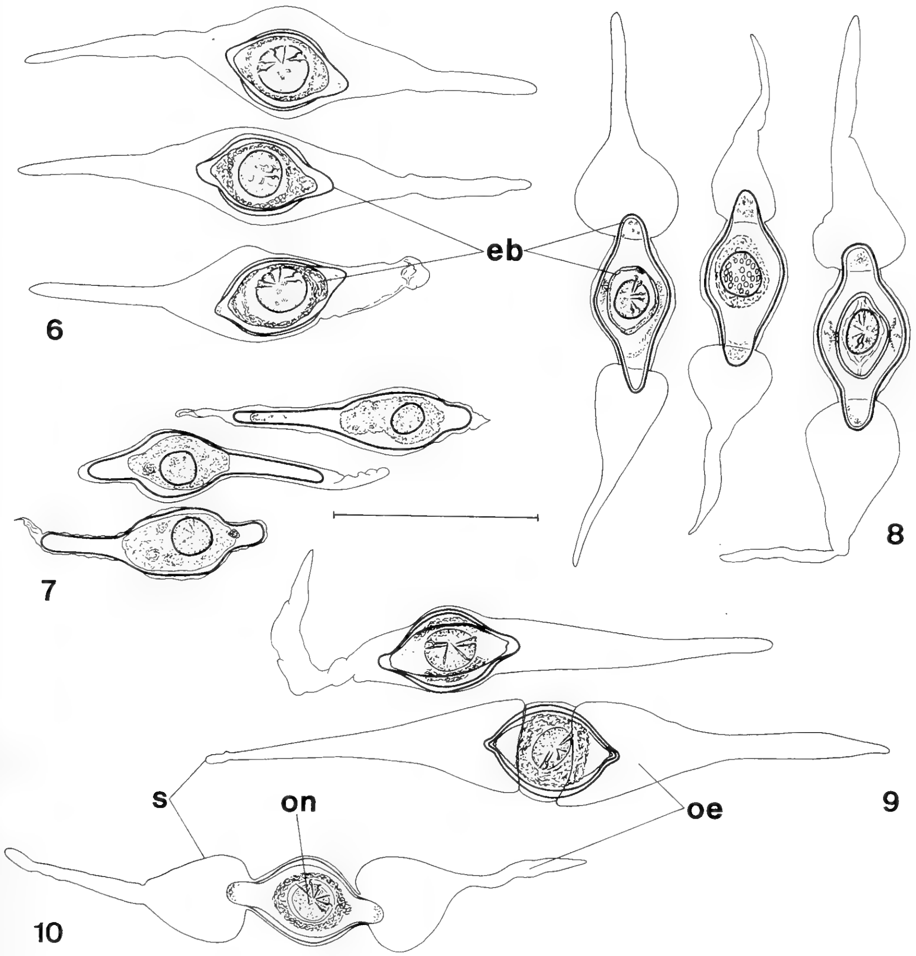
Genital pores alternating irregularly, in 21-32% (n = 6) of proglottis length. Cirrus pouch thin-walled, 170-205 long. Cirrus pouch length occupying 16-22% (n = 4) of proglottis width. Vas deferens not reaching body midline in mature proglottis.

Vagina posterior (53%) or anterior (47%) to cirrus pouch, with inconspicuous terminal muscular sphincter. Ovary medullar, bilobed, strongly lobed and bearing dorsal projections penetrating the cortex; occupying 60-72% of proglottis width. Vitelline follicles distributed cortically and ventrally, in two lateral bands, sometimes reaching anterior and posterior margin of proglottis, with a tendency of posterior concentration, uninterrupted by cirrus pouch and vagina.

Uterine primordium like a medullar cylindrical mass of chromophil cells. Lumen appearing from the first mature proglottides until formation of eggs. Uterine branches occupying up to 56% of proglottis width, with 8-12 lateral branches on each side, 1or 2 layered. Eggs with two polar projections.

Remarks: The new species belongs to *Rudolphiella* Fuhrmann, 1916 based on the cortical distribution of the testes and vitelline follicles, on the medullar position of uterus, as well as on the medullar and partially cortical location of the ovary (Rego, 1994). Four species of *Rudolphiella* are present: *R. lobosa* (Riggenbach, 1895) recorded in *Luciopimelodus pati*; *R. myoides* (Woodland, 1934) and *R. piranabu* (Woodland, 1934), both parasites of *Pinirampus pirinampu*; *Rudolphiella piracatinga* (Woodland, 1935), parasite of *Calophysus macropterus*. *Rudolphiella* cf. *lobosa* de Chambrier & Vaucher, 1999 parasite of *Megalonema platanum* is also considered.

Rudolphiella szidati sp. n. differs from all described species in the genus by the size of metascolex and by the testes number (Table 1). Furthermore, in *R. szidati*, (with *R. lobosa* and *R.* cf. *lobosa*) testes laterally reaching the posterior end of proglottis, while in *R. myoides* and *R. piranabu* the number of testes decreases and they do not



FIGS 6-10

Rudolphiella spp., Eggs drawn in distilled water. 6. *Rudolphiella piranabu* (Woodland, 1934), 25129 INVE; 7. *Rudolphiella myoides* (Woodland, 1934), 24712 INVE; 8. *Rudolphiella szidati* sp. n., 24670 INVE; 9. *Rudolphiella piracatinga* (Woodland, 1935), 19650 INVE; 10. *Rudolphiella* cf. *lobosa*, 22352 INVE (de Chambrier & Vaucher, 1999, fig. 95). Several eggs are not totally ripe. Abbreviations: eb = bilayered embryophore, oe = outer envelope, on = oncosphere, s = shell. Scale-bar, 50 μm

reach the posterior end of proglottis (de Chambrier & Vaucher, 1999; Pavanelli & Machado dos Santos, 1992; Riggenbach, 1895; Woodland, 1934, 1935).

Within the genus *Rudolphiella*, the eggs have a similar pattern with elongated poles, *R. szidati* (Fig. 8), *R. piracatinga* (Fig. 9), *R.* cf. *lobosa* (Fig. 10) and *R. piranabu* (Fig. 6) possess poles of similar size, but the shape is different in the 4 taxa; in *R. myoides*, one pole is shorter than the other (Fig. 7). The oncospheres of the 4 known species are similar in size (9-13), the outer envelope is difficult to compare among species based on uncertainties in the descriptions by different authors.

DISCUSSION

As we observed some more characters which are shared by all *Rudolphiella* species (i.e. presence of glandular cells within the apex, vagina anterior/posterior, shape of eggs), we gave above a new diagnosis of the genus.

Luciopimelodus pati is a common dweller fish of the Paraguay river, Bermejo river, Paraná river, Uruguay river, Carcarañá river and de la Plata river. The distribution of 3 Pimelodidae sharing the same common name (« patí »), *Megalonema platanum* (Günther, 1880), *Pinirampus pirinampu* (Spix, 1829) and *Luciopimelodus pati* (Valenciennes, 1840) is overlapping (Ringuelet *et al.*, 1967). Since we were unable to find the species of parasites described by Riggenbach (1895) (neither *R. lobosa* nor *Proteocephalus fossatus*), from *L. pati*, we suspect that the host studied by Riggenbach was not *Luciopimelodus pati*, but possibly *Megalonema platanum*; this host was studied for cestodes by de Chambrier & Vaucher (1999) and it was parasited by *Rudolphiella* cf. *lobosa*.

Rego (1975) described *Monticellia rugata* from *Calophysus macropterus* in Amazonia. This cestode is a mixture of the two species *Nomimoscolex piracatinga* Woodland, 1935 and *Monticellia piracatinga* Woodland, 1935. The figures 44, 45, 47, 49 and 50 belong to *Monticellia piracatinga* and figures 46 and 48 belong to *Nomimoscolex piracatinga*. This latter species was transfered to the genus *Monticellia* under the name *Monticellia amazonica* by de Chambrier & Vaucher (1997). «Piracatinga» is the vernacular name given to *Calophysus macropterus* in Amazonia and to *Luciopimelodus pati* in high Paraná river in Brazil. Fowler (1951) and Ringuelet *et al.* (1967) placed *L. pati* into the Paraná bassin, but not in the Amazon bassin. We think that Woodland could be mistaken in attributing the name piracatinga to *L. pati* in Amazonia. Our recently collected material in Amazonia from *Calophysus macropterus* fits with the type material of the two species described by Woodland (*M. piracatinga* and *N. piracatinga*) and seems to confirm our hypothesis. *Monticellia rugata* Rego, 1975 is thus a junior synonym of *Monticellia piracatinga*. However, the study of type material of *M. piracatinga* Woodland, 1935 revealed that this species belongs to the genus *Rudolphiella*, as it is confirmed by the recent collected material from *Calophysus macropterus* in the Amazon and becomes *Rudolphiella piracatinga* (Woodland, 1935) comb. nov.

So far, numerous proteocephalideans possess unicelullar glands in the scolex (de Chambrier *et al.*, 1992, 1996; de Chambrier & Vaucher, 1997, 1999; Gil de Pertierra,

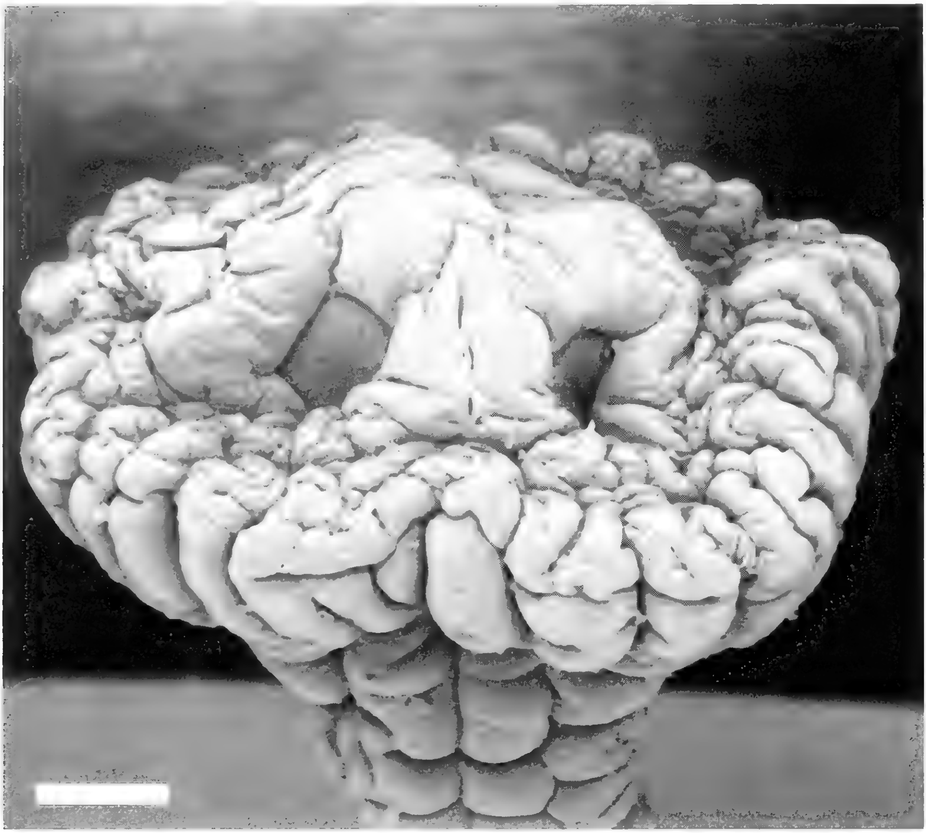


FIG. 11
Scolex, *Rudolphiella szidati* sp. n., 24669 INVE. Scale-bar, 200 µm.

1995; Gil de Pertierra & Viozzi, 1999; Scholz *et al*., 1998, 1999; Stoitsova *et al*., 1995). These glands are also present in all known species of *Rudolphiella* in high number and arranged in a cross, with granular inclusions. Zd´árská & Nebesárová (1999) give a detailed description of the unicellular glands situated under the apex of the scolex in *Proteocephalus macropterus*.

The presence of *R. myoides* and *R. piranabu* was confirmed in the host *Pinirampus pirinampu* from Amazon river by one of the authors (A. de Chambrier), and *R. piranabu* was confirmed by Pavanelli & Machado Dos Santos (1992) in the same host from Paraná river, Brazil.

Brooks (1984, 1995) already demonstrated, in phylogenetic analyses based on morphological characters, the monophyly of three *Rudolphiella* species (*R. lobosa*, *R. myoides* and *R piranabu*) based on the presence of elongated egg. However, his 1995 analysis showed some homoplasious characters and is consequently somewhat less

TABLE 1. Comparative mèasures of *Rudolphiella* species.

Genus *Rudolphiella*	*R. szidati* sp. n.	*R. lobosa* syntypes	*R. piracatinga* syntypes	*R. piranabu* syntypes	*R. myoides* syntypes	*R.* cf. *lobosa* (de Ch.+V. 1999)
Hosts	*Luciopimelodus pati*	"*Pimelodus pati*"	*Calophysus macrocephalus*	*Pinirampus pirinampu*	*Pinirampus pirinampu*	*Megalonema platanum*
Basin	Parana	Parana	Amazon	Amazon	Amazon	Parana
ø metascolex	1735-2970	1025-1350	340-360 *	580-680	590	925-1700
ø suckers	395-595	205-245				305-345
% PC	15-32, m = 23	16-22, m = 18				21-23, m = 22
% ovary	43-68, m = 53	60-72, m = 65				54-62, m = 58
% genital pore	20-46, m = 30	21-32, m = 27				18-26, m = 21
testes number	289-365, m = 325	194-219, m = 206	40-50	+ 100 (80**)	100	180-183
nb. uterine diverticles	9-17	8-12				4-10
nb. of proglottis	22-37	35	15	15	15	25-27
Total length	16-27 mm, m = 22	17-22 mm	6 mm	10 mm	11 mm	10 mm
Vagina position***	77% posterior	53% posterior		81% posterior	33% posterior	28% posterior

* distorded in mounting according to Woodland (1935)
** according to Pavanelli & Machado dos Santos (1992)
*** position of vagina in comparison with cirrus pouch

supported. We observed that all *Rudolphiella* species shown some more synapomorphies: presence of glandular cells with granular inclusions arranged in a cross situated between the suckers and the tegument, eggs with elongated shell, embryophores bearing two polar projections, vitellines follicles cortical in two ventral bands situated sub-laterally, vagina anterior/posterior. Those synapomorphies shared by all *Rudolphiella* species emphasize the homogeneity of this group and enforced the Brooks' opinion on the monophyly of this genus.

Stewart (1986) stated that *Luciopimelodus pati*, *Pinirampus pirinampu* and *Calophysus macropterus* belong to a monophyletic group called the «Calophysus group», within the Pimelodidae, opinion confirmed by Lundberg *et al.* (1991) and more recently by de Pinna (1998). On the other hand, *Megalonema* shares some characteristics with the *Calophysus* group, and other groups closely related to Diplomystidae (primitive catfishes). In the light of our studies, the presence of *Rudolphiella* cf. *lobosa* (de Chambrier & Vaucher, 1999) from *Megalonema platanum* confirms the relationship of *M. platanum* with the *Calophysus* group.

In conclusion, the sole genus *Rudolphiella* is widespread among the genera of the «*Calophysus* group» we studied, including *Megalonema platanum*. It is, worthwhile to emphasize that it could be a likely case of coevolution between related species of hosts and their parasites.

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Two new species of the genus *Suffasia* from Sri Lanka (Araneae: Zodariidae)

Suresh P. BENJAMIN[1] & Rudy JOCQUÉ[2]

[1] Institut für Natur-, Landschafts- und Umweltschutz der Universität Basel (NLU), Abteilung Biologie, St. Johanns-Vorstadt 10
CH-4056 Basel, Switzerland.

[2] Koninklijk Museum voor Midden-Afrika, B-3080 Tervuren, Belgium.

Two new species of the genus *Suffasia* from Sri Lanka (Araneae: Zodariidae). - Two new species of the genus *Suffasia* Jocqué, 1991 are described. *S. mahasumana* sp. n. is known from both sexes and is related to *S. tumegaster* Jocqué, 1992. *S. attidiya* sp. n., known only from two female specimens, may be related to *S. tigrina* (Simon, 1893). *S. attidiya* sp. n. is found in diverse habitats, *S. mahasumana* sp. n. is confined to cloud forests in the central highlands of Sri Lanka. This is the first record of *Suffasia* from Sri Lanka, other species in this genus are known only from southern India and Nepal.

Key-words: Araneae - Zodariidae - *Suffasia* - tropical montane cloud forests - Sri Lanka.

INTRODUCTION

The genus *Suffasia* was established for two species from southern India. The type species, *S. tigrina* (Simon, 1893) from Kodaikanal, Tamil Nadu, and an undescribed species from the same locality (Jocqué, 1991). *S. tumegaster* Jocqué, 1992, from Kathmandu, Nepal, was added later. Considering the affinities of the faunas of India and Sri Lanka it was to be expected that members of *Suffasia* or at least of closely related genera might be discovered on the island.

During recent field work in Sri Lanka two undescribed species were collected. The first one is from the Knuckles Range, consisting of a number of remnant patches of primary tropical montane cloud forests, a type of vegetation that was once common in the central highlands of Sri Lanka. Most of these forests were cleared for tea plantations during the British colonial period. The second species was collected in fragmented marshland situated on the outskirts of Colombo. On both localities the specimens were obtained by beating shrubs and small trees which is an unusual way to collect zodariids as they are considered soil dwelling spiders except for the representatives of the Storenomorphinae (Jocqué, 1991). In the Bellanwila-Attidiya sanctuary a marshy area near Colombo, shrubs are scattered around shallow water ponds, marshes and sea-

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sonally flooded grassland. A female of the second new species was collected by the same method in Kalugala, Labugama Forest Reserve, a fragmented remnant of tropical lowland rain forest, some 40 km away from the former locality.

METHODS

Structures were examined in temporary mounts embedded in glycerine. Vulvae were cleared with trypsin (0.1% trypsin, 0.1% $CaCl_2$, in 0.05M tris-buffer, pH 7.6). All drawings were made with a Nikon Labophot-2 and a Nikon SMZ-U microscopes with drawing tube. Measurements are in mm. Structures examined with the scanning electron microscope (PHILIPS XL30 FEG ESEM) were critical point dried, stud-mounted and sputter coated for observation and photography. Specimens examined are deposited in the "Muséum d'histoire naturelle, Genève" (MHNG) and the "Naturhistorisches Museum, Basel" (NMB).

Abbreviations used in the text and figures: AER anterior eye row; ALE anterior lateral eyes; AME anterior median eyes; CD copulatory duct; CF cymbial flange; CO copulatory opening; E embolus; FD fertilisation duct; PER posterior eye row; PLE posterior lateral eyes; PME posterior median eyes; TA tegular aphophysis.

Suffasia mahasumana sp. n. Figs 1-7, 13-21

Holotype ♂: Sri Lanka, Central Province, Knuckles Range, Deenston (approximately 7° 19' N, 80° 51' E), 1100 m, 11 March 1998. Leg. Suresh P. Benjamin (MHNG).

Paratypes: 1♀, 11 March 1998 (MHNG); 1♂, 1♀ 12 March 1998 (NMB); further as holotype.

Etymology: Named after god Maha-Sumana, protector of the hill country in Sri Lanka. Noun in apposition.

Diagnosis: *S. mahasumana* is closely related to *S. tumegaster*; the male can be recognised by the absence of a dorsal spike on the palpal tibia, the shape of the dorsal cymbial flange which is flat and evenly rounded in the latter, swollen, curved upwards and concave in the former; the female differs from that of *S. tumegaster* by the presence of a roughly rectangular plate in the anterior part of the epigyne.

Description: Male (holotype). Colouration and markings: carapace dark yellow-brown, with dark reticulations on anterior part and with U-shaped dark marking in front of fovea (Fig. 14). Chelicerae and sternum dark yellow, lighter than carapace. Dorsum of opisthosoma uniform darkgrey, venter white, without markings. Legs light yellow with dark dorsal markings. AER almost straight, PER slightly procurved, all eyes circular, AME 1.5 times their diameter apart from each other and at about the same distance from ALE. PME 2 times their diameter apart and about the same distance from PLE. ALE = PLE = PME > AME. Clypeus height 6 times the diameter of ALE. Chilum present. Chelicerae not fused, with double-tooth on promargin. Labium triangular. Sternum sub triangular, with spike-like extensions projecting towards base of coxae. Leg formula 4132, 2 spines dorsally on femora I-IV. Tibiae with flattened incised hairs (Fig. 16, FIS); and ventral tuft of metatarsal preening brush with chisel-shaped hairs (Figs 16, 17, CH; see also Jocqué, 1991: figs 6, 8, 11, 12). Femoral organ (Fig. 20) present on each leg. Trichobothrium base with concentric ridges (Fig. 15).

Palp (Figs 1-4): Tibia with stout, sharp, strongly tapered retrolateral apophysis, pointing outwards. Cymbium strongly narrowed in dorsal view, with swollen, upwards curved, dorsolateral flange (Fig. 1, CF), extending lateral cymbial concavity, carrying some sensorial hairs in superior part; embolus fairly short, stout, originating on posterior part of tegulum separated from main part by shallow groove; tegular apophysis, short, stout, sharp, pointing out and forwards (Figs 1, 2, TA).

Measurements: total length: 2.3; carapace length: 1.3; carapace width: 1.0. Legs:

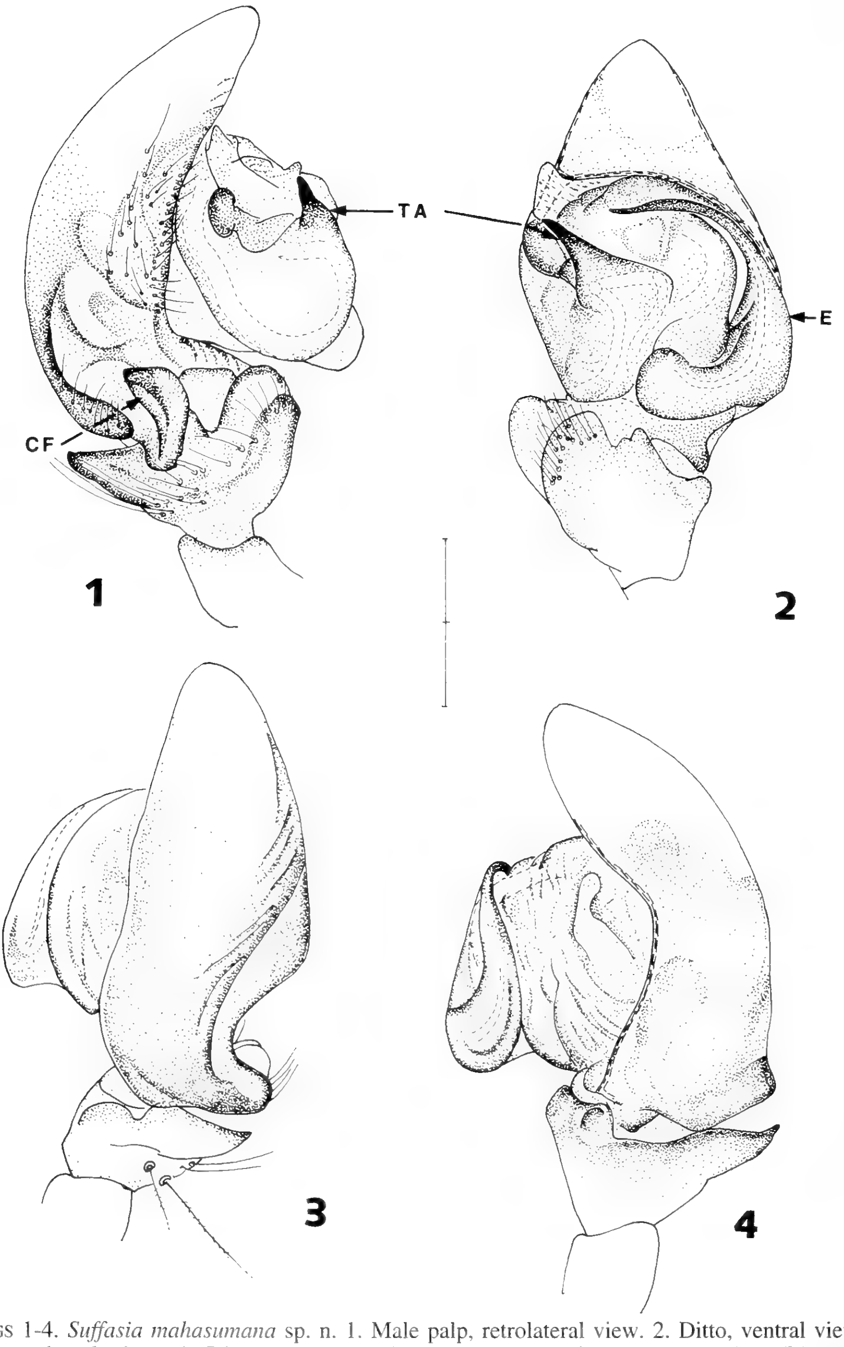
	I	II	III	IV
femur	1.1	0.9	1.0	1.1
patella	0.2	0.2	0.3	0.3
tibia	1.0	0.7	0.7	1.0
metatarsus	1.1	0.9	1.0	1.5
tarsus	0.5	0.4	0.4	0.5
total	3.9	3.1	3.4	4.4

Female. Colouration and markings: Similar to male but lighter. Different by possessing dorsal opisthosomal markings as in Fig. 13; venter white. Palp with conical tarsus, longer than tibia (Fig. 19). Morphology further as in male.
Epigynum and vulva (Figs 5-7): Simple brown plate in anterior part; internal structure visible through thin tegument; copulatory openings in front hidden by plate; short copulatory ducts lead to thick-walled spermathecae, triangular in dorsal view.

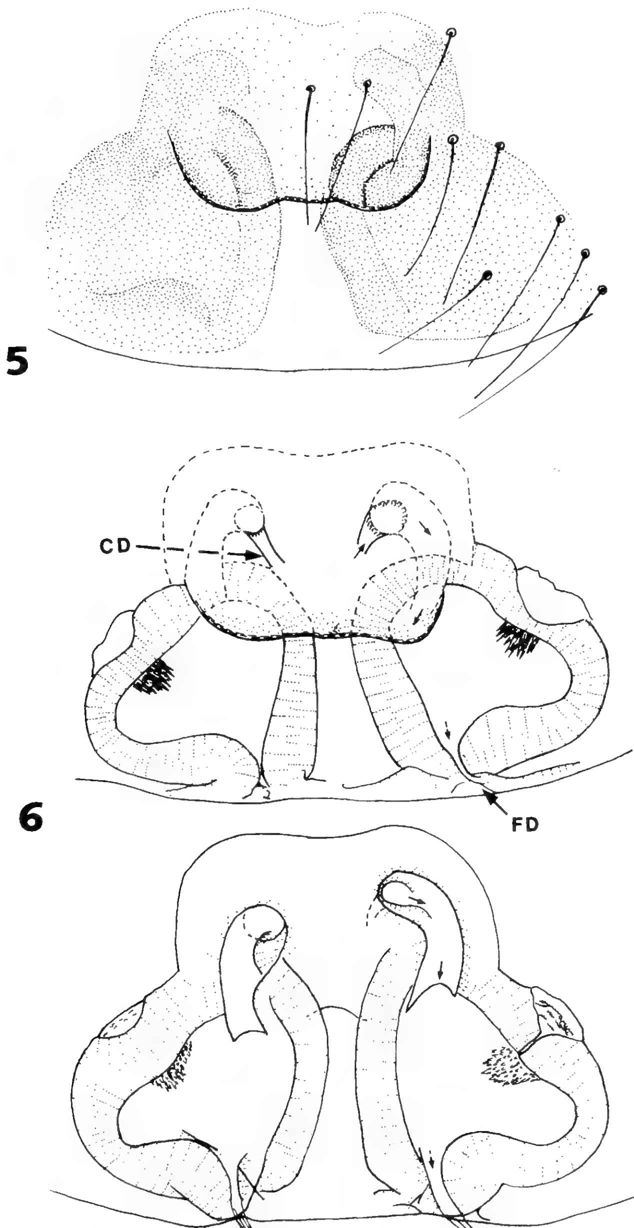
Measurements: Total length: 3.0; carapace length: 1.3; carapace width: 1.0. Legs:

	I	II	III	IV
femur	0.8	0.8	0.9	1.1
patella	0.3	0.3	0.4	0.4
tibia	0.8	0.7	0.6	0.8
metatarsus	0.9	0.7	0.8	1.2
tarsus	0.5	0.4	0.4	0.5
total	3.3	2.9	3.1	4.0

Affinities: *Suffasia* is defined by the presence of a chilum and promarginal cheliceral teeth, dark reticulation ("network pattern" *sensu* Jocqué, 1992), female palp with a long conical tarsus, femoral organ with simple setae on all legs, legs with flattened incised hairs and metatarsal preening brush consisting of chisel-shaped hairs (Jocqué, 1991, 1992). The present species clearly agrees with these characters and can thus be attributed to *Suffasia*. Yet the shape of the male palpal cymbium casts some doubt on this attribution. Although one of the main characteristics of *Asceua* Thorell, 1887 is exactly the strongly narrowed cymbium, there are a number of characters that exclude the incorporation of the present species in it: representatives of that genus do indeed



FIGS 1-4. *Suffasia mahasumana* sp. n. 1. Male palp, retrolateral view. 2. Ditto, ventral view. 3. Ditto, dorsal view. 4. Ditto, prolateral view. CF cymbial flange; E embolus; TA tegular apophysis. Scale line: 0.2 mm.



FIGS 5-7. *Suffasia mahasumana* sp. n. 5. Female epigynum, ventral view. 6. Vulva, ventral view. 7. Ditto, dorsal view. CD copulatory duct; FD fertilisation duct. Scale line: 0.1 mm.

lack teeth, have a uniform dark carapace and lack femoral organs. Yet, both *S. mahasumana* and *S. tumegaster* possess an epigynum that is quite different from what has been described for *Suffasia*. It might prove necessary to erect a new genus for these species if the male of type species of *Suffasia* appears equally different which was already recognised by Jocqué (1992).

Distribution: Known only from the type locality.

Suffasia attidiya sp. n. Figs 8-12

Holotype ♀: Sri Lanka, Western Province, Colombo, Bellanwila-Attidiya (approximately 6°50'N, 79°54'E), mean elevation 0.6 m asl, 22 February 1998, (MHNG).

Paratype ♀: Sri Lanka, Western Province, Kalugala, Labugama Forest Reserve, 3 August 1996, ca. 10 m (NMB). All specimens leg. Suresh P. Benjamin.

Etymology: Named after the type locality. Noun in apposition.

Diagnosis: The epigyne of *S. attidiya* differs from that of *S. tigrina* by the course of the copulatory ducts which run directly inwards in the latter, outwards thence inwards in the new species. *S. mahasumana* is clearly different by the presence of a plate in the epigyne.

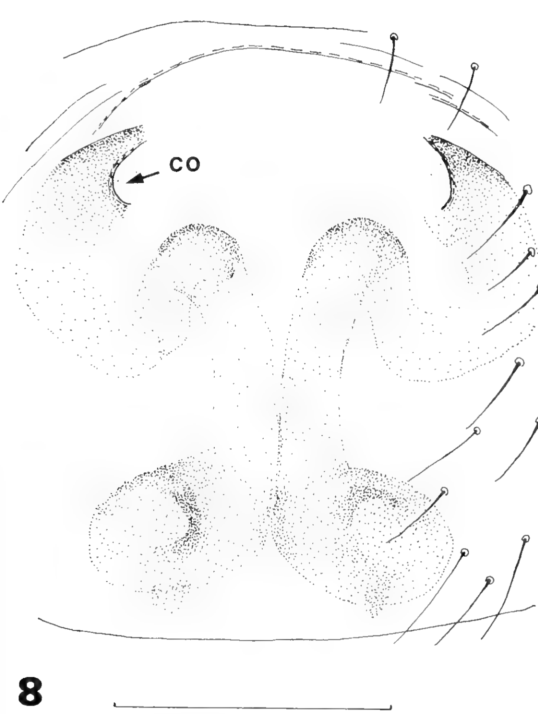
Description: Female (holotype). Colouration and markings: prosoma dorsally dark yellow-brown, with dark markings in front of fovea (Fig. 12). Chelicerae and sternum dark yellow lighter than dorsal prosoma. Dorsum of opisthosoma with markings as in Fig. 11, venter white. Legs light yellow with dark dorsal markings. AER slightly procurved, PER procurved, all eyes circular, AME 1.5 times their diameter apart from each other, 0.5 times from ALE. PME 2 times their diameter apart and 2.5 times from PLE. ALE = PLE = PME > AME. Clypeus height 6 times the diameter of ALE. Chilum present; chelicerae not fused, with double tooth on promargin. Labium triangular. Sternum sub triangular, with spike-like extensions projecting towards base of coxae. Palp with conical tarsus, longer than tibia. Flattened incised hairs on tibiae; ventral tuft of metatarsal preening brush with chisel-shaped hairs.

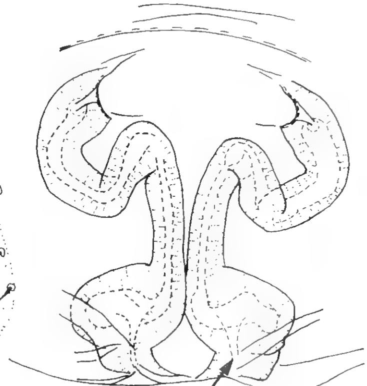
Epigynum and vulva (Figs 8-10): Epigynum simple, anterior sclerotized border with CO situated laterally. Thick-walled copulatory ducts straight and close to each other in posterior part, leading to small globular rectptacula, with thick walls. FD as in Fig. 9.

Male. Unknown.

Affinities: As zodariid genera are mainly diagnosed on male palpal morphology (Jocqué, 1991, 1992) the placement of this new species of *Suffasia* might appear ambiguous. However, the similarities of the epigynum of the present species and of the type species are so striking that there is little doubt that they are congeneric. In both cases the internal structure is simple with lateral CO, strongly sclerotized CD with a partly parallel course and roughly oval spermathecae.

FIGS 8-14. *Suffasia attidiya* sp. n. (8-12). *Suffasia mahasumana* sp. n. (13, 14). 8. Female epigynum, ventral view. 9. Vulva, ventral view. 10. Ditto, dorsal view. 11. Female opisthosoma, dorsal view. 12. Female prosoma and right palp, dorsal view. 13. Female, dorsal view. 14. Male, dorsal view. CO copulatory opening; FD fertilisation duct. Scale lines: 0.1 mm (8-10), 2.0 mm (11-14).





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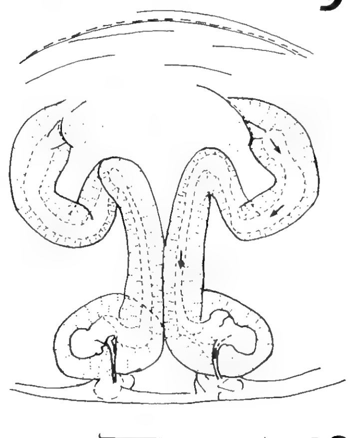

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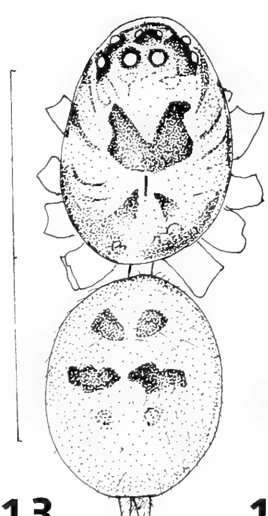

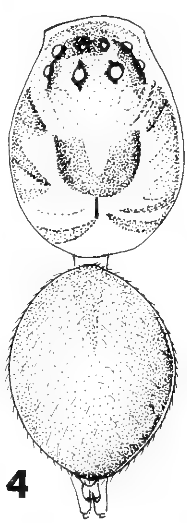

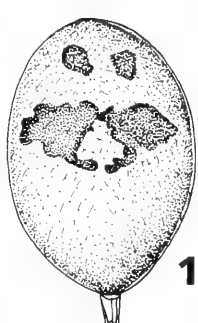

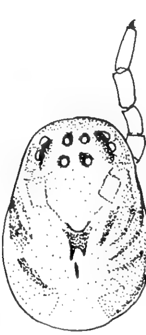

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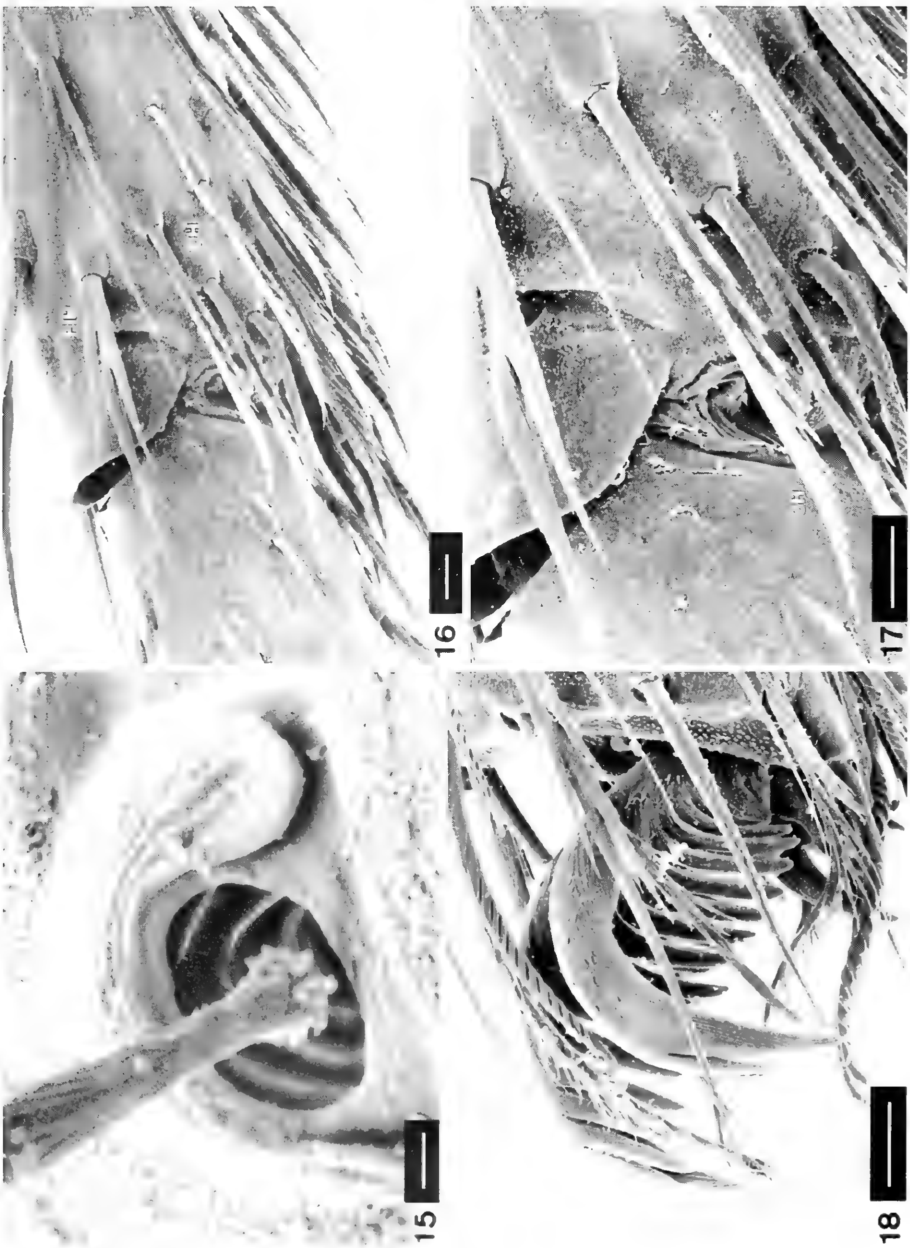
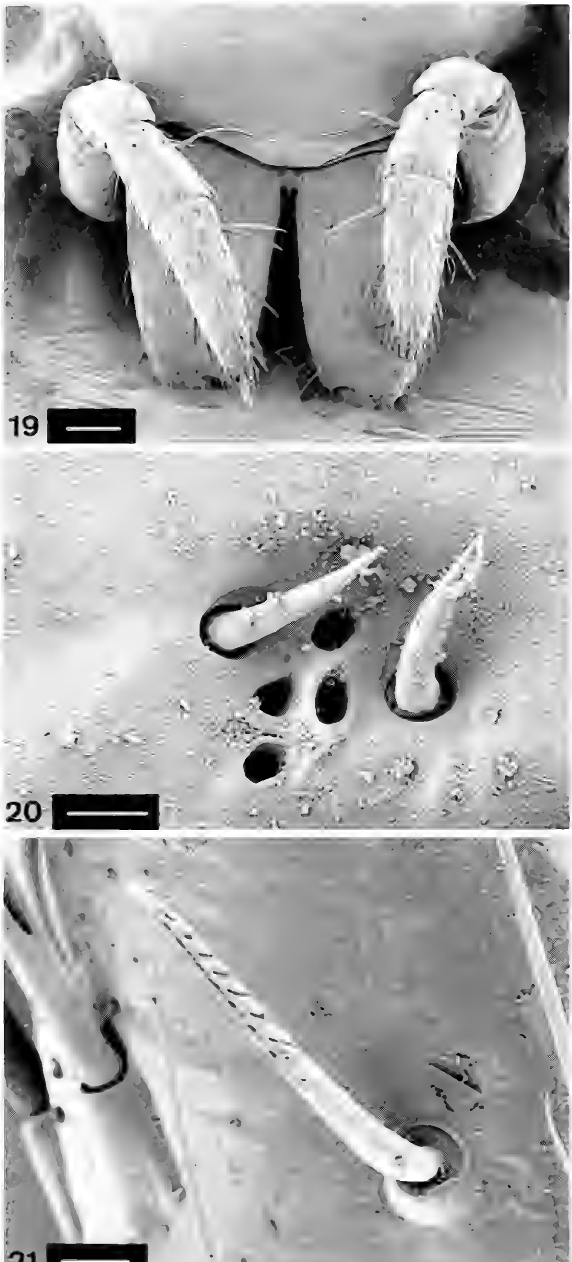


FIGS 15-18. *Suffasia mahasumana* sp. n., SEM micrographs. 15. Base of trichobothrium. 16. Preening brush on distal metatarsus of leg I, lateral view. 17. Ditto, detail. 18. Tip of leg I, lateral view. CH chisel-shaped hairs. FIS flattened incised hairs. Scale lines: 0.001 mm (1), 0.01 mm (16-18).



FIGS 19-21. *Suffasia mahasumana* sp. n., SEM micrographs. 19. Chelicerae and palps of female, frontal view. 20. Femoral organ, on leg I. 21. Chemosensitive hair on metatarsus. Scale lines: 0.003 mm (20), 005 mm (21), 0.1 mm (19).

Measurements: Total length: 2.6; carapace length: 1.3; carapace width: 1.0. Legs:

	I	II	III	IV
femur	0.6	0.5	0.6	0.7
patella	0.1	0.1	0.2	0.2
tibia	0.5	0.4	0.4	0.6
metatarsus	0.6	0.5	0.5	0.8
tarsus	0.4	0.3	0.3	0.4
total	2.2	1.8	2.0	2.7

Distribution: Known from Bellanwila-Attidiya sanctuary and Kalugala, Labugama Forest Reserve.

DISCUSSION

The placement of the two new species in the genus *Suffasia* is in accordance with the current definition of the genus. However the relationships proposed here should be re-analysed when additional material, most importantly the male of *S. tigrina* is discovered.

In his revision of the Zodariidae Jocqué (1991) considered the subfamilies Zodariinae and Storeninae to be monophyletic. This hypothesis was based on presumed autapomorphies such as the presence of a femoral organ and flattened incised hairs for the Zodariinae and chisel-shaped hairs on the metatarsal preening brush for Storeninae. The discovery of *S. tumegaster*, which possesses a combination of all these characters, led to an amalgamation of these two subfamilies (Jocqué, 1992). *S. mahasumana* sp. n. which also possesses these three characters, further confirms his combination of both subfamilies.

The discovery of the new taxa extends the previously known distribution (Nepal, India) of the genus *Suffasia* southwards to Sri Lanka.

ACKNOWLEDGEMENTS

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Diversité du zoobenthos dans 47 rivières du canton de Vaud: tendance 1989 - 1997

Claude LANG
Conservation de la faune, Marquisat 1, CH-1025 St-Sulpice, Suisse.
claude.lang@sffn.vd.ch

Diversity of zoobenthos in 47 rivers of western Switzerland: the 1989 - 1997 trend. - Three surveys of benthic invertebrates were made between 1989 and 1997 in 165 sites located in 47 rivers of western Switzerland (canton of Vaud). Eight descriptors derived from the total number of taxa and the number of taxa intolerant of pollution (Plecoptera, Heptageniidae, and Trichoptera with a case) were used to describe the patterns of benthic diversity. In the three surveys, the diversity increased with the altitude of sampling sites. This trend reflected the upward decrease of human impact on the rivers and their watersheds. The diversity increased between 1989 and 1997 because of better meteorological conditions (i.e. more water in the rivers) coupled with the increased efficiency of sewage treatment plants. But the diversity remained low in several small rivers, probably because of chronic pollutions by pesticides.

Key-words: diversity - indicator species - river - water quality - zoobenthos.

INTRODUCTION

Depuis la signature de la convention sur la diversité biologique à Rio de Janeiro en 1992, la conservation et la restauration de la diversité des espèces dans l'espace et le temps constituent un des buts fondamentaux de l'écologie appliquée (Wright *et al.*, 1998). Dans le même ordre d'idée, la diversité des communautés d'invertébrés qui colonisent le fond des cours d'eau (zoobenthos) est utilisée depuis le début du siècle pour caractériser l'état du milieu: elle diminue en fonction de l'intensité des perturbations subies, que celles-ci soient d'origine humaine ou naturelle (Hellawell, 1986).

Cette diminution de la diversité est particulièrement marquée chez les plécoptères, certains éphéméroptères et les trichoptères à fourreau d'où l'utilisation de ces groupes comme indicateurs (Fore *et al.,* 1996). Dans les rivières du canton de Vaud par exemple, la diversité des plécoptères a fortement diminué entre 1945 et 1982 à basse altitude alors qu'elle ne changeait guère dans les rivières de montagne, restées proches de l'état naturel (Aubert, 1984). Ce gradient de diversité amont-aval reflète l'augmentation des impacts d'origine humaine à basse altitude (Lang & Reymond, 1993, 1995).

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Entre 1982 et 1997, l'épuration des eaux s'est généralisée et les performances des stations d'épuration se sont améliorées dans le canton de Vaud (Fiaux *et al.*, 1998). De ce fait, les quantités de matière organique et de nutriments déversées dans les cours d'eau ont diminué. La diversité du zoobenthos devrait donc augmenter en réponse à cette amélioration de la qualité chimique de l'eau.

Il ne faut toutefois pas oublier que le bassin versant et la rivière qui le draîne, forment un tout: ce qui affecte l'un, modifie l'autre (Hynes, 1975). Du fait de cette relation étroite, le caractère de moins en moins naturel des bassins versants, surtout à basse altitude, pourrait empêcher la restauration de la diversité, même si la composition chimique de l'eau redevient normale, tout au moins en termes d'éléments majeurs (matière organique, phosphore et azote); les micropolluants constituant en effet un problème à part (Corvi & Kim-Heang, 1997; Vioget & Strawczynski, 1997).

Pour interpréter l'évolution à long terme du zoobenthos, il faut également tenir compte de la météorologie (Allan, 1995). Par exemple, une sécheresse de longue durée va réduire le débit des cours d'eau et augmenter ainsi la concentration des polluants, donc leur impact sur le zoobenthos. Faute d'une dilution suffisante, les capacités d'auto-épuration naturelles de certains cours d'eau peuvent être complètement dépassées si l'épuration des eaux n'a pas été conçue en fonction de conditions extrêmes. Ces dernières pourraient s'observer plus fréquemment si le climat venait à changer rapidement sous l'influence de l'effet de serre. Signalons également que des crues très violentes, comme une longue sécheresse, peuvent durablement diminuer la diversité du zoobenthos en bouleversant le lit des cours d'eau (Allan, 1995).

La présente étude analyse l'évolution de la diversité du zoobenthos dans les rivières vaudoises sur la base de trois campagnes de prélèvements effectuées entre 1989 et 1997. Son but consiste à mettre en évidence l'effet sur le zoobenthos des mesures d'assainissement prises, ceci en fonction de l'altitude et des conditions météorologiques observées au cours de cette période.

STATIONS ET MÉTHODES

Le zoobenthos des rivières vaudoises est étudié depuis 1982 (Lang & Reymond, 1995). Cependant le réseau de surveillance, sous sa forme actuelle, n'a été mis en place qu'à partir de 1989. De ce fait l'analyse présentée ici se concentre sur une période où les données sont parfaitement comparables entre elles: 165 stations de prélèvements étudiées au cours de trois campagnes effectuées entre 1989 et 1997 dans 47 rivières.

Les 47 rivières étudiées (Fig. 1) sont réparties en trois groupes d'après la région où chacune d'elles prend sa source: (1) le Jura et l'ouest du canton de Vaud, (2) le Jorat et le centre du canton, (3) les Préalpes et les Alpes. La Broye, l'Arbogne et la Mionne sont rattachées aux rivières du Jorat en raison de leur ressemblance avec celles-ci. Dans le Jura, 20 rivières et 75 stations de prélèvement ont été visitées en 1990, 1993 et 1996 (Lang, 1997); dans le Jorat, 15 rivières et 47 stations visitées en 1991, 1994 et 1997 (Lang, 1998); dans les Alpes, 12 rivières et 43 stations visitées en 1989, 1992 et 1995 (Lang, 1996). Seules les rivières et les stations visitées au cours des trois campagnes sont incluses dans la présente étude.

FIG. 1

Localisation et numéros d'identification des 47 rivières vaudoises visitées entre 1989 et 1997.

1 Doye	11 Saubrette	21 Talent	31 Bressonne	41 Gryonne
2 B. de Nyon	12 B. Morges	22 Buron	32 Carrouge	42 P. Gryonne
3 Asse	13 Morges	23 Mentue	33 Grenet	43 Avançon
4 Promenthouse	14 Venoge	24 Sauteru	34 Mionne	44 Hongrin
5 Colline	15 Veyron	25 Petite Glâne	35 Forestay	45 Sarine
6 Cordex	16 Nozon	26 Broye	36 Veveyse	46 Flendruz
7 Serine	17 Orbe	27 Arbogne	37 B. Clarens	47 Torneresse
8 Dullive	18 Mujon	28 Lembe	38 B. Montreux	1 - 20 Jura
9 Aubonne	19 Arnon	29 Cerjaule	39 Tinière	21 - 35 Jorat
10 Toleure	20 Baumine	30 Mérine	40 Grande Eau	36 - 47 Alpes

Les 165 stations de prélèvements étudiées ont été choisies parce qu'elles présentent des caractéristiques communes qui les rendent comparables entre elles: pour la plupart, elles sont localisées dans la zone à truite de Huet et le rithron d'Illies, donc

TABLEAU 1. Calcul de la valeur de l'indice RIVAUD à partir du nombre total de taxons (NT) et du nombre de taxons sensibles aux pollutions (NTS). La valeur de RIVAUD se lit à l'intersection de la ligne renfermant la valeur de NT et de la colonne où se trouve la valeur de NTS. Exemple: NT = 19, NTS = 7, RIVAUD = 11. Source: Lang & Reymond (1995).

	NTS										
NT	0	1	2	3	4	5	6-7	8-9	10-11	12-13	14-25
1-4	1	2	3	4	5	-	-	-	-	-	-
5-8	2	3	4	5	6	7	8	9	-	-	-
9-12	3	4	5	6	7	8	9	10	11	12	-
13-16	4	5	6	7	8	9	10	11	12	13	14
17-20	5	6	7	8	9	10	11	12	13	14	15
21-24	6	7	8	9	10	11	12	13	14	15	16
25-28	7	8	9	10	11	12	13	14	15	16	17
29-32	8	9	10	11	12	13	14	15	16	17	18
33-36	9	10	11	12	13	14	15	16	17	18	19
37-50	10	11	12	13	14	15	16	17	18	19	20

Qualité biologique mauvaise (RIVAUD 1 - 5), faible (6 - 9), médiocre (10 - 11), moyenne (12 - 14), bonne (15 - 20).

dans une écorégion relativement homogène (Ribaut, 1966); toutes renferment des surfaces de cailloux balayées par le courant (zone de rapides) d'au moins 20 m^2 ce qui permet de prélever toujours dans le même substrat; aucune n'est directement exposée aux rejets polluants d'une station d'épuration ou d'un important égout: elles représentent donc la situation générale de la rivière en l'absence de pollutions ponctuelles bien marquées.

Dans le Jura et le Jorat, chaque station est visitée à deux reprises chaque année d'étude: la première fois en janvier-février, la seconde fois en mars-avril, c'est-à-dire pendant l'étiage d'hiver et avant la crue de printemps. Dans les Alpes, la première campagne s'effectue en février-mars pendant l'étiage hivernal, la deuxième en juin après la crue de printemps et la troisième en septembre en période de basses eaux. Trois visites par année sont nécessaires dans les Alpes. Certaines stations ne sont en effet pas accessibles en hiver à cause de la neige et la glace, en juin à cause des hautes eaux et en septembre parce que le niveau d'eau est trop bas pour prélever. De plus, du fait du caractère torrentiel de ces cours d'eau, l'abondance de la faune y est souvent très faible ce qui fait qu'une visite peut ne pas être représentative.

Au cours de chaque visite, six coups de filet sont donnés dans six différentes zones de cailloux (rapides) de la station, correspondant chacune à une surface prélevée d'environ 0.1 m^2. Le filet est posé sur le fond, son ouverture (20 cm x 20 cm) face au courant, de manière à ce que celui-ci y entraîne les invertébrés délogés en remuant le substrat avec le pied. Tous les invertébrés récoltés dans ces six coups de filet constituent un prélèvement qui est immédiatement conservé sur le terrain dans du formol 5 %.

En laboratoire, les invertébrés, séparés des sédiments et débris végétaux par des tamisages successifs (Reymond, 1995), sont identifiés et comptés jusqu'au niveau du genre, de la famille ou de la classe selon les groupes (Annexe 1). La liste combinée des

taxons présents chaque année dans chaque station est ensuite dressée à partir des deux ou trois (Alpes) prélèvements effectués dans chacune d'elles; cependant, le même taxon observé dans les deux ou trois prélèvements de la même station n'est compté qu'une seule fois. Toutes les analyses présentées dans cet article sont basées sur la liste combinée des taxons présents la même année dans la même station. Cette approche rend les comparaisons entre stations et entre années plus fiables en diminuant l'impact d'évènements exceptionnels (brèves crues avant le prélèvement par exemple) sur la diversité du zoobenthos (Furse *et al.*, 1984).

Dans cette étude, la diversité des communautés d'invertébrés est estimée à partir de huit descripteurs: (1) le nombre total de taxons (genre ou famille), (2) le nombre de taxons sensibles aux pollutions (plécoptères, heptagéniidés et trichoptères à fourreau), (3) le rapport nombre de taxons sensibles sur nombre total de taxons (2/1 en %), (4) l'indice RIVAUD calculé à partir de 1 et 2 (Tab 1), (5) le nombre de familles, (6) le nombre de familles sensibles aux pollutions (plécoptères, heptagéniidés et trichoptères à fourreau), (7) le rapport nombre de familles sensibles sur nombre total de familles (6/5 en %), (8) l'indice de diversité de Margalef (Magurran, 1988) dont l'expression est:

Diversité = (nombre de familles -1) / ln du nombre d'individus récoltés.

Les descripteurs retenus ici sont ceux généralement utilisés pour l'étude des cours d'eau (Fore *et al.*, 1996). Certains sont très semblables entre eux (1 à 3 et 5 à 7): tout ce qui les différencie, c'est le niveau d'identification atteint (le genre ou la famille). Leur inclusion permet d'évaluer l'effet de ce facteur sur l'analyse des résultats.

Les diversités calculées ici ne sont pas basées sur les espèces mais sur des genres, des familles et même des classes (Annexe 1). Cependant cette approche simplifiée peut être utilisée parce qu'il existe une corrélation très significative entre le nombre de familles et d'espèces présentes dans les rivières (Wright *et al.*, 1998). De plus, l'analyse des communautés d'invertébrés benthiques donne souvent des résultats analogues qu'elle soit basée sur des identifications faites au niveau au niveau de la famille ou de l'espèce (Furse *et al.*, 1984).

Les variations des huit descripteurs sont analysées en fonction de l'altitude des 165 stations de prélèvements, de la région où celles-ci se trouvent (Jura, Jorat et Alpes) et de la date des campagnes de prélèvements. Trois campagnes sont comparées entre elles: 1989-1991, 1992-1994, 1995-1997. Quatre zones d'altitude sont définies à partir des valeurs quartiles (25 %, 50 %, 75 %) et extrêmes de l'altitude des stations de prélèvements.

En plus de l'analyse basée sur les stations, les valeurs moyennes des huit descripteurs sont calculées pour chaque rivière et pour chaque campagne de prélèvements afin d'évaluer la tendance rivière par rivière. Pour ce faire, la valeur du coefficient de corrélation de rang de Spearman est calculée entre les trois valeurs moyennes de chaque descripteur et les dates correspondantes des trois campagnes de prélèvements. Le nombre de rivières où la valeur du descripteur augmente régulièrement (r_s = 1.00) est ensuite comparée à celui des rivières où sa valeur diminue (rs = - 1.00) au moyen du test binomial. Les rivières où les valeurs de r_s sont autres que +1 ou -1 sont exclues de la comparaison.

RÉSULTATS

Le tableau 2 présente l'évolution des valeurs moyennes des huit descripteurs du zoobenthos en fonction de trois critères: l'altitude, la région et la date des campagnes de prélèvements. Nous constatons tout d'abord que les valeurs moyennes des huit descripteurs augmentent significativement avec l'altitude des stations de prélèvement. C'est entre 375 m et 449 m d'altitude, dans la zone où les impacts des activités humaines sont les plus forts (Lang & Reymond, 1995), que les valeurs observées sont les plus basses. Nous observons ensuite que, dans les rivières des Préalpes et des Alpes, les nombres moyens des taxons et des familles sensibles aux pollutions sont nettement plus élevés dans que dans celles du Jura et du Jorat. Comme la diversité totale est la même dans les trois régions, le pourcentage de taxons et de familles sensibles aux pollutions est plus élevé dans les rivières de montagne qu'ailleurs. Dans l'interprétation

TABLEAU 2. Valeurs moyennes par station de 8 descripteurs du zoobenthos en fonction de l'altitude, de la région et de la campagne de prélèvements. Descripteurs: nombre total de taxons d'invertébrés (NT), nombre de taxons sensibles aux pollutions (NTS), pourcentage de taxons sensibles aux pollutions (PNTS), indice RIVAUD, nombre de familles (NF), nombre de familles sensibles aux pollutions (NFS), pourcentage de familles sensibles aux pollutions (PNFS), indice de diversité de Margalef (DIV). Au sein d'un même ensemble et d'une même variable, les moyennes qui ne sont pas significativement différentes au seuil de 5 %, sont indiquées par des lettres semblables. Ensembles 1 et 2 basés sur tous les résultats 1989 - 1997.

Ensembles comparés		Valeurs moyennes par station								
		N[a]	NT	NTS	PNTS	RIVAUD	NF	NFS	PNFS	DIV
1. Altitude (m)	375-449	43	18.9A	3.6A	17.2A	8.4A	17.4A	2.9A	15.6A	2.16A
	450-539	43	24.1B	7.0B	27.9B	12.3B	20.9B	5.2B	24.4B	2.52B
	540-699	48	25.3B	7.8B	29.2B	12.9B	21.7B	5.6B	25.2B	2.57B
	700-1410	41	26.1B	10.4C	40.9C	14.7C	22.0B	7.1C	33.4C	2.80C
2. Région	Jura[b]	75	22.9A	6.0A	23.7A	11.1A	20.1A	4.5A	21.0A	2.43A
	Jorat[c]	47	24.3A	6.4A	24.2A	11.8A	21.2A	4.8A	21.4A	2.53A
	Alpes[d]	43	23.7A	10.0B	42.2B	13.9B	20.2A	6.7B	34.0B	2.62A
3. Campagne	1989-1991	165	21.7A	6.4A	28.0A	11.1A	19.0A	4.8A	24.4A	2.38A
	1992-1994	165	22.6A	7.0A	29.1A	11.8A	19.7A	5.1A	24.7A	2.46A
	1995-1997	165	26.2B	8.0B	28.9A	13.2B	22.6B	5.7B	24.4A	2.68B

[a] Nombre de stations
[b] Altitude des stations: 375 - 1040 m, moyenne: 522 m
[c] Altitude des stations: 430 - 775 m, moyenne: 555 m
[d] Altitude des stations: 380 - 1410 m, moyenne: 882 m

des résultats, il faut noter que les effets de l'altitude et de la région sont souvent mêlés. Par exemple, les valeurs moyennes observées entre 700 m et 1410 m d'altitude correspondent en majeure partie aux rivières des Alpes et des Préalpes; les valeurs observées en-dessous de 450 m, aux rivières du Jura. Remarquons enfin que les valeurs moyennes de six des huit descripteurs du zoobenthos augmentent entre 1989 et 1997. C'est entre la deuxième et la troisième campagne de prélèvements que l'augmentation est particulièrement marquée.

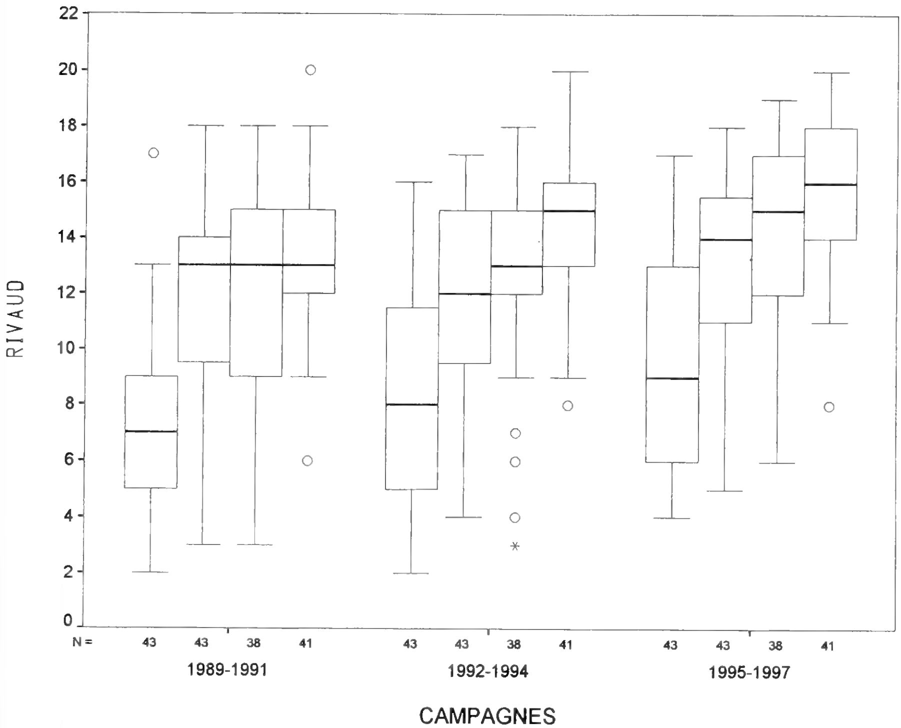

FIG. 2

Variations des valeurs quartiles (petits côtés du rectangle de bas en haut: 25%, 50%, 75%) et extrêmes (lignes) de l'indice RIVAUD en fonction de l'altitude des stations de prélèvements au cours des trois campagnes effectuées entre 1989 et 1997. Les cercles et les étoiles indiquent des valeurs aberrantes excédant 1.5 fois l'espace interquartile. Pour chaque campagne, les stations sont réparties en 4 classes d'altitude de gauche à droite: 375 - 449 m, 450 - 539 m, 540 - 669 m, 700 - 1410 m. N = nombre de stations par classe d'altitude.

Les figures 2 et 3 montrent d'une part que les valeurs quartiles de l'indice RIVAUD et du nombre de familles augmentent régulièrement avec l'altitude des stations dans deux des trois campagnes de prélèvements comparées, d'autre part que les différences entre les trois campagnes sont également significatives (analyse de variance: effet de l'altitude, P = 0.001; effets de la campagne, P = 0.001). Remarquons cependant que, pour la campagne 1989 - 1991, les valeurs médianes de la diversité sont les mêmes dans les trois dernières zones d'altitude. Cette répartition particulière semble indiquer que la sécheresse exceptionnelle de 1989 a exercé une influence négative sur la diversité du zoobenthos (Fig. 4).

La corrélation positive ($r_s = 0.82$) qui existe entre le nombre de taxons sensibles aux pollutions et le nombre total de taxons présents dans les 47 rivières vaudoises étudiées entre 1989 et 1997 (Fig. 5), permet de classer celles-ci en fonction de la

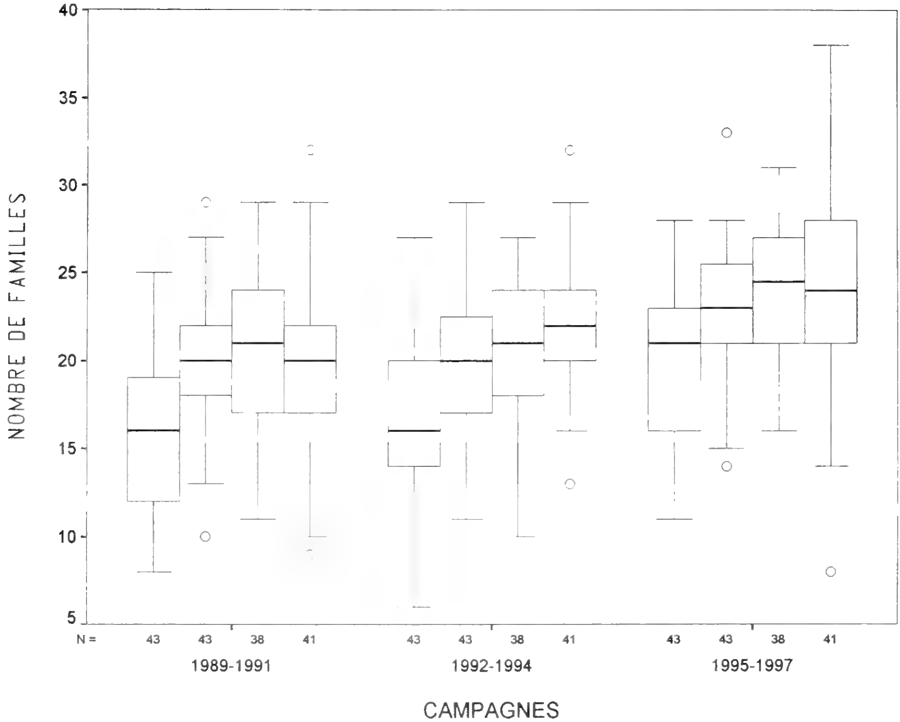

FIG. 3

Variations des valeurs quartiles et extrêmes du nombre de familles d'invertébrés en fonction de l'altitude des stations de prélèvements au cours des trois campagnes effectuées entre 1989 et 1997 (légende, voir Fig. 2).

diversité du zoobenthos. En bas et à gauche de la figure, nous trouvons de petites rivières, situées en général à basse altitude, dans des paysages très modifiés par l'homme: la Dullive, la Petite Glâne, la Morges et le Boiron de Morges. En haut à droite, nous observons des rivières de montagne comme l'Hongrin et la Torneresse qui drainent des bassins versants relativement peu modifiés par l'homme, tout au moins en amont des stations étudiées. Certaines rivières de montagne, notamment l'Avançon, la Tinière, la Veveyse et la Grande Eau, occupent une position marginale sur la figure 5. La diversité des taxons sensibles aux pollutions (surtout celle des plécoptères) y est très élevée par rapport à la diversité totale. Cette situation particulière s'explique par un caractère torrentiel accentué qui élimine de nombreux taxons. Comparons enfin la faible diversité observée dans la Venoge à la diversité élevée de son principal affluent le Veyron. Si la qualité de l'environnement s'améliorait à basse altitude, la situation de la Venoge devrait se rapprocher de celle du Veyron.

L'évolution de la diversité du zoobenthos entre 1989 et 1997, pour les 47 rivières étudiées, est présentée dans le tableau 3 avec les valeurs moyennes des huit descripteurs utilisés. Sur les 376 tendances calculées (8 descripteurs multipliés par 47

TABLEAU 3. Valeurs moyennes et tendances de 8 descripteurs du zoobenthos calculées pour chacune des 47 rivières vaudoises visitées à 3 reprises entre 1989 et 1997. Tendance: augmentation (+), diminution (-), aucune tendance (0). Descripteurs: nombre total de taxons (NT), nombre de taxons sensibles aux pollutions (NTS), pourcentages des taxons sensibles aux pollutions (PNTS), indice RIVAUD, nombre total de familles (NF), nombre de familles sensibles aux pollutions (NFS), pourcentage des familles sensibles aux pollutions (PNFS), indice de diversité de Margalef (DIV).

	Rivière	Valeurs moyennes (en dessus) et tendances (en dessous)							
No	(Stations)	NT	NTS	PNTS	RIVAUD	NF	NFS	PNFS	DIV
1	Doye	15.3	1.7	11	5.7	15.3	1.7	11	1.9
	(1)	0	0	0	0	0	0	0	0
2	B. de Nyon	15.7	1.8	10.6	6	15.1	1.8	11	1.9
	(4)	0	0	0	0	0	0	0	0
3	Asse	19.4	3.8	16.5	8.3	17.8	3.1	15.6	2.1
	(4)	+	0	0	+	+	0	0	+
4	Promenthouse	23.8	6.7	27.2	12	21.1	4.9	22.8	2.6
	(3)	+	+	+	+	+	+	+	0
5	Colline	25.3	7.5	28.3	13	21.8	5.5	24.7	2.7
	(2)	0	+	+	0	0	+	+	0
6	Cordex	26.3	9.7	36.6	14.7	23.3	7	30	2.8
	(1)	+	+	+	0	0	0	0	-
7	Serine	20	6.2	30.6	11	18.7	4.8	26.3	2.3
	(2)	0	0	-	0	0	0	0	0
8	Dullive	10.7	0.5	5.2	3.5	10.7	0.5	5.2	1.3
	(2)	0	0	0	+	0	0	0	0
9	Aubonne	27.2	9.3	33.9	14.5	22.9	6.2	27.3	2.7
	(5)	+	0	0	+	+	+	0	0
10	Toleure	26.8	10.3	38.6	14.8	22.8	7.5	33	2.9
	(2)	0	+	+	0	0	0	0	-
11	Saubrette	18.3	4.7	25.3	10	17.7	4	22.9	2.1
	(1)	0	0	0	0	0	0	0	0
12	B. Morges	18	2.6	13.2	7.5	17.2	2.5	13.4	2.1
	(5)	0	0	+	0	0	0	+	0
13	Morges	18	3	16.1	8	17.1	2.9	16.5	2
	(5)	0	-	-	0	0	0	0	0
14	Venoge	21.3	4.5	19.5	9.8	19	3.5	17.2	2.4
	(14)	+	0	0	+	+	0	0	+
15	Veyron	30.9	10.2	32.9	15.8	24.8	7.3	29.2	3
	(4)	+	+	0	+	+	0	0	+
16	Nozon	28.9	10.8	37.1	15.7	23.4	7.4	31.6	2.7
	(6)	0	+	0	0	0	+	0	0
17	Orbe	27.3	6.3	22.9	12.5	23.3	5.1	21.7	2.8
	(5)	+	+	+	+	+	+	+	+
18	Mujon	17.3	2	11.4	7	17.3	2	11.4	1.9
	(1)	0	0	-	0	0	0	-	-
19	Arnon	30.9	10.2	32.9	15.8	24.8	7.3	29.2	3
	(7)	0	0	+	+	0	0	+	0
20	Baumine	28.7	5.7	19.3	13	25	4.7	18.3	2.8
	(1)	0	0	0	0	0	0	0	0
21	Talent	19	4.1	18.4	8.6	17.7	3.4	17.3	2
	(7)	+	+	+	+	+	+	+	+
22	Buron	23.5	6.3	27.1	12	20.7	4.7	22.8	2.5
	(2)	0	0	0	0	0	0	0	0
23	Mentue	27.5	8.5	30	14.1	22.9	5.8	24.5	2.7
	(8)	0	0	0	0	0	0	0	0

TABLEAU 3 (suite)

No	Rivière (Stations)	NT	NTS	PNTS	RIVAUD	NF	NFS	PNFS	DIV
		Valeurs moyennes (en dessus) et tendances (en dessous)							
24	Sauteru	29	7.8	27.1	14.2	26	6.2	24	3.1
	(2)	0	0	+	0	0	0	0	0
25	Petite Glâne	15.8	1.2	7.3	5.5	15.6	1.2	7.3	2
	(4)	0	+	+	+	0	+	+	0
26	Broye	27.4	7	24.4	13.1	23.4	5.3	22	2.8
	(7)	+	0	0	+	+	0	0	+
27	Arbogne	23.9	5	20.4	11	21	3.9	18.1	2.5
	(3)	+	+	+	+	0	+	+	0
28	Lembe	15.7	2.7	16.5	7	15.3	2.7	16.9	1.9
	(1)	0	-	0	-	0	-	-	0
29	Cerjaule	25.7	8.3	32.4	13.7	23	7	30.5	2.8
	(1)	0	-	0	-	0	-	0	-
30	Mérine	31.3	11.7	37.1	16.7	25.7	8	31.2	3.1
	(1)	0	0	0	0	0	0	-	0
31	Bressonne	27.8	9.3	32.6	14.4	23.6	6.7	28	2.9
	(3)	+	+	+	+	0	+	+	+
32	Carrouge	21.3	4.8	21.4	10.2	19.5	4	20	2.2
	(2)	0	0	0	0	0	0	0	-
33	Grenet	26.4	8.2	30.8	13.8	22.8	6.2	27.1	2.7
	(4)	0	0	0	0	0	0	-	+
34	Mionne	29.7	10.3	34.7	15.7	24.7	7.7	31.1	2.9
	(1)	0	0	0	0	0	0	+	0
35	Forestay	22.3	3	12.7	9	20.3	3	14.1	2.4
	(1)	0	0	0	0	0	0	0	0
36	Veveyse	22	8.7	39.3	13	18	5	27.7	2.4
	(1)	+	0	0	+	+	0	0	+
37	B. Clarens	29.4	11.2	37.9	15.8	24.8	7.6	30.4	2.9
	(4)	0	0	0	0	+	0	0	+
38	B. Montreux	27.6	11.1	40.3	15.7	23.6	7.2	30.6	2.9
	(3)	0	0	0	0	0	0	-	+
39	Tinière	19.7	7.9	38.8	11.6	17.4	5.7	32.2	2.3
	(3)	0	0	0	0	0	0	0	0
40	Grande Eau	20.8	9.5	45.7	13	17.9	6.7	37.9	2.4
	(10)	+	+	0	0	0	0	-	0
41	Gryonne	23.8	8.9	37.6	13.6	20.8	6.1	29.6	2.7
	(4)	0	0	-	0	0	-	-	+
42	P. Gryonne	25	8	32	13.3	22.3	5.7	25.2	2.7
	(1)	0	+	+	0	0	0	+	+
43	Avançon	17.4	7.9	45.4	11.2	15.2	5.7	37.7	2.2
	(7)	+	+	-	+	0	+	-	+
44	Hongrin	32.7	12.5	38.1	17.3	26.7	8	30	3.2
	(2)	+	+	0	+	+	+	0	+
45	Sarine	26.8	11	42.2	15.2	22.3	7.5	34.6	2.8
	(4)	+	0	0	+	+	0	0	+
46	Flendruz	28	12.3	44.1	16.3	23	8	35.2	3
	(1)	+	+	0	+	+	0	-	+
47	Torneresse	30	14.1	47	17.3	24.1	8.6	35.5	2.9
	(3)	0	0	0	0	0	0	0	+
	Tendance (+/-)	(17/0)	(16/3)	(13/5)	(18/2)	(13/0)	(11/3)	(11/9)	(18/5)
	Probabilité	0	0.004	0.096	0	0	0.057	0.824	0.012

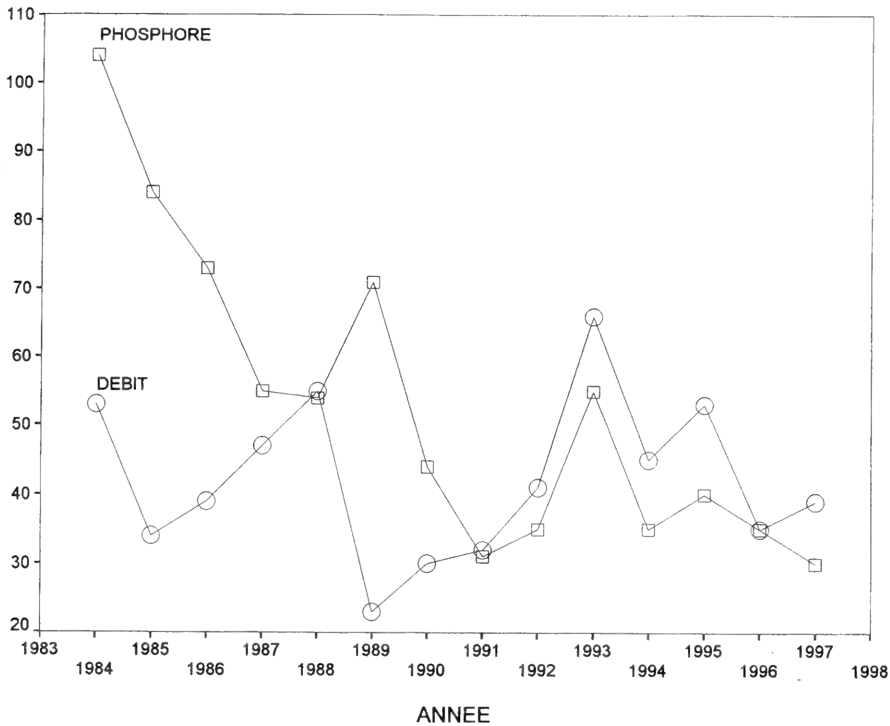

FIG. 4

Evolution des concentrations moyennes en phosphore soluble (mg / m^3) et des débits d'eau (m^3 / sec multipliés par 10) dans la Venoge entre 1984 et 1997. Les concentrations sont pondérées par le débit (Orand *et al.*, 1998).

rivières), 117 indiquent une augmentation de la valeur du descripteur et 27 une diminution (test binomial, P = 0.001); dans 232 cas, aucune tendance bien marquée n'est observable. Lorsque les tendances sont analysées descripteur par descripteur (colonne par colonne), les nombres d'augmentations sont significativement supérieurs à ceux des diminutions pour six descripteurs sur huit. Pour les pourcentages de taxons ou de familles sensibles aux pollutions, les différences ne sont pas significatives, ce qui suggère que ces deux descripteurs sont moins efficaces que les six autres pour détecter une tendance. Lorsqu'on examine l'évolution de la diversité rivière par rivière (ligne par ligne), la tendance dominante est clairement visible dans la plupart des cas, même si l'ensemble des huit descripteurs n'indiquent le même diagnostic que dans dix rivières. Les diagnostics contradictoires (une augmentation et une diminution dans la même rivière) sont également rares: ils sont le fait de l'indice de Margalef et du pourcentage de taxons ou de familles sensibles aux pollutions, descripteurs dont la valeur indicatrice a déjà été mise en doute ci-dessus.

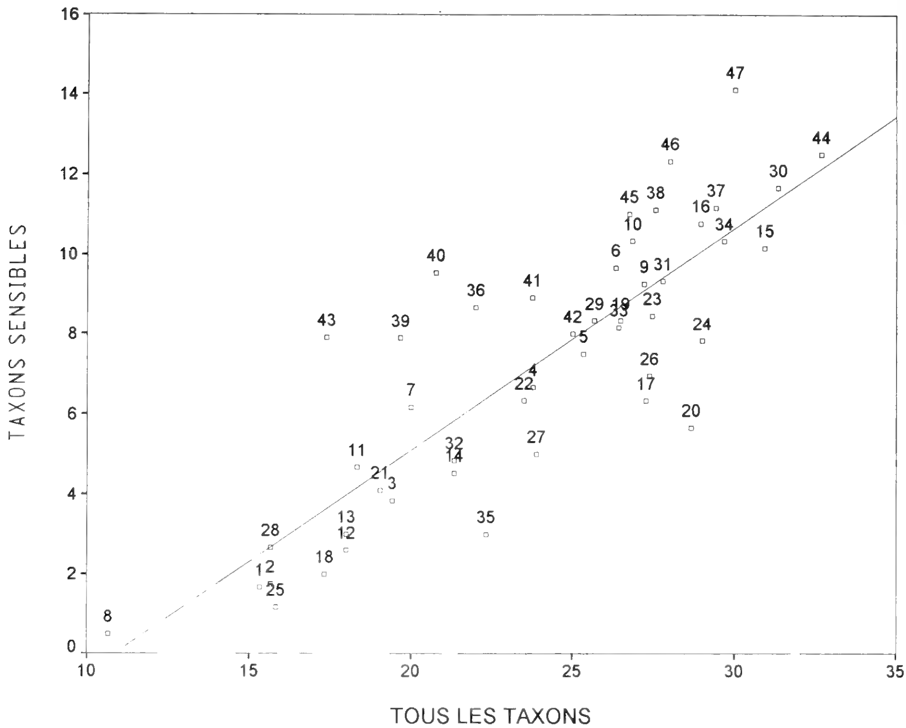

FIG. 5

Relation entre le nombre total de taxons d'invertébrés et le nombre de taxons sensibles aux pollutions (plécoptères, heptagéniidés et trichoptères à fourreau), permettant de classer les 47 rivières vaudoises visitées entre 1989 et 1997, les unes par rapport aux autres en fonction de leur diversité (voir Tab. 3, numéros d'identification et noms des rivières).

DISCUSSION

Dans les rivières vaudoises, la diversité du zoobenthos augmente d'une part en fonction de l'altitude des stations de prélèvements dans chacune des trois campagnes effectuées entre 1989 et 1997, d'autre part en fonction du temps écoulé entre la première et la troisième campagnes (Figs 2, 3). La première tendance correspond à l'augmentation amont-aval des perturbations d'origine humaine qui s'observe dans la plupart des bassins versants vaudois (Lang & Reymond 1993, 1995). La deuxième tendance montre à la fois les progrès de l'épuration des eaux et les effets d'une météorologie favorable.

L'épuration des eaux a permis de contrôler efficacement certains polluants ainsi que l'illustre la baisse significative ($r_s = - 0.84$, n = 14) des concentrations en phosphore soluble dans la Venoge entre 1984 et 1997 (Fig. 4). Cette figure montre également que la longue sécheresse de 1989 a momentanément compromis l'amélioration de la qualité

chimique de l'eau. En effet cette année-là, le débit moyen de la Venoge est particulièrement faible, comme d'ailleurs celui des autres rivières vaudoises. A cause de ce manque d'eau, les apports en phosphore soluble, ainsi que ceux d'autres polluants, sont moins dilués et les concentrations plus élevées qui en résultent, affectent davantage le zoobenthos (Allan, 1995).

La situation météorologique extrême de 1989 a influencé fortement la première des trois campagnes de prélèvements effectuées entre 1989 et 1997 (Figs 2, 3). L'évolution ultérieure de la diversité pourrait ainsi s'interpréter comme le rétablissement progressif du zoobenthos après un épisode climatique exceptionnel. Si cette interprétation est correcte, la diversité du zoobenthos observée pendant la dernière campagne correspondrait à une situation normale sur le plan météorologique pour les rivières vaudoises. En prenant les diversités observées en altitude comme valeurs de référence pour un milieu où les perturbations d'origine humaine sont minimes (Figs 2, 3), nous constatons une sérieuse baisse de la diversité à basse altitude, ceci malgré une épuration des eaux complètement réalisée (Fiaux *et al.*, 1998).

L'effet de l'amélioration de la qualité chimique de l'eau sur la diversité du zoobenthos serait ainsi contrecarré par la persistance d'autres perturbations d'origine humaine (Allan, 1995). Citons entre autres: l'alluvionnement, l'altération des débits de crue et d'étiage et la dégradation de la végétation riveraine. En un mot, tout ce qui modifie le caractère naturel d'un cours d'eau et de son bassin versant fait diminuer la diversité du zoobenthos. Le milieu naturel environnant les rivières vaudoises est dégradé mais l'étendue de sa dégradation ne peut pas être évaluée, faute d'une base de référence et de données quantitatives précises. Cependant, l'influence de l'agriculture et de l'urbanisation est évidente.

Les activités agricoles pratiquées dans le bassin versant influencent la diversité du zoobenthos. L'évolution d'une rivière américaine illustre ce point (Grubaugh & Wallace, 1995): après la disparition dans le bassin versant d'une agriculture intensive (utilisant beaucoup d'engrais, de pesticides et provoquant une forte érosion), la diversité du zoobenthos a fortement augmenté. Dans le canton de Vaud, l'évolution inverse s'est produite entre 1960 et 1970 avec le passage d'une agriculture traditionnelle à une agriculture intensive (B. Reymond, com. pers.). Il est significatif de constater que la diversité des plécoptères, insectes particulièrement sensibles à l'influence humaine (Fore *et al.*, 1996), a fortement diminué entre 1945 et 1982 dans le cours inférieur de la Venoge, du Talent, de la Broye et d'autres cours d'eau traversant des paysages agricoles très modifiés par l'homme (Aubert, 1984).

En plus des effets à long terme de l'agriculture sur le paysage, des pollutions tant aiguës que chroniques par des produits phytosanitaires pourraient expliquer la faible diversité du zoobenthos qui persiste entre 1989 et 1997 dans certaines rivières vaudoises où l'épuration des eaux est entièrement réalisée. Citons, par exemple, le Boiron de Nyon, l'Asse, la Dullive, le Boiron de Morges et la Morges (Tab. 3). En raison de la conjonction de faibles débits et d'une agriculture très active, divers produits phytosanitaires sont présents dans l'eau en concentrations relativement élevées (Corvi & Kim-Heang, 1997; Vioget & Strawczynski, 1997). De plus, des déversements acci-

dentels de ces produits provoquent fréquemment la mort des poissons et des invertébrés, parfois seulement celle des invertébrés; dans ce cas, les pollutions et leurs auteurs sont particulièrement difficiles à détecter (Ph. Tavel, com. pers.).

En plus de ces pollutions aiguës mais sporadiques, les concentrations en phytosanitaires mesurées dans ces cours d'eau suggèrent qu'il pourrait exister une pollution chronique. Celle-ci agirait de façon subtile sur le taux de survie des espèces. Par exemple, le nombre de trichoptères du genre *Limnephilus*, capables d'émerger de l'eau et donc de se reproduire, diminue significativement en présence d'une très faible concentration (1 ng/l) de lindane, un insecticide (Schulz & Liess, 1995). Il est bien clair que des effets si subtils ne peuvent pas être mis en évidence par des méthodes classiques de surveillance biologique des eaux.

Le zoobenthos des rivières vaudoises subit également les effets négatifs d'une urbanisation accrue, surtout à basse altitude. En effet, la densité de la population humaine qui constitue un bon indicateur des impacts liés à l'urbanisation (Statzner & Sperling, 1993), augmente en général d'amont en aval dans les bassins versants du canton de Vaud (Lang & Reymond, 1995). Une forte densité humaine entraîne par exemple: (1) l'augmentation des surfaces de sol imperméables ce qui modifie les débits de crue et d'étiage, facteurs critiques pour le zoobenthos; (2) l'accroissement du réseau de canalisations qui conduisent les eaux usées aux stations d'épuration (Statzner & Sperling, 1993). Plus ce réseau est étendu, plus la matière organique et les polluants peuvent s'y accumuler par temps sec; de ce fait, plus grand sera l'impact de ces dépôts sur la rivière après une forte pluie, sauf si les déversoirs d'orage sont conçus et entretenus de façon optimale.

En conclusion, Statzner & Sperling (1993) suggèrent qu'une rivière épurée, son bassin versant et la population qui l'habite constituent un système complexe qu'il faudrait gérer comme un tout, en utilisant différentes approches, si l'on veut améliorer à moindre coût la qualité biologique de l'eau. C'est une conception analogue qui devrait être adoptée à l'avenir dans les rivières vaudoises.

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ANNEXE 1. Fréquence des taxons identifiés entre 1989 et 1997. Source: Lang 1996, 1997, 1998. Taxons présents +, 1 - 10% des prélèvements, fréquents ++, 11 - 50%, très fréquents +++, 51 - 100%, - absent. L'astérisque signale les taxons sensibles aux pollutions.

Taxons[a]	Région Jura	Jorat	Alpes
TURBELLARIA			
Planariidae			
Polycelis	++	+	+
Dugesiidae			
Dugesia	++	++	++
Oligochaeta	+++	+++	+++
HIRUDINEA			
Glossiphonidae			
Helobdella	+	+	-
Glossiphonia	+	+	-
Erpobdellidae			
Erpobdella	++	++	+
MOLLUSCA			
Hydrobiidae	+	-	+
Ancylidae	++	++	-
Limnaeidae	++	+	+
Sphaeriidae	++	++	+
Physidae	+	-	-
Bythinellidae	+	-	-
Bithyniidae	-	-	+
HYDRACARINA	+++	++	++
CRUSTACEA			
Gammaridae	+++	+++	++
Asellidae	+	+	+
EPHEMEROPTERA			
Ephemeridae			
Ephemera	+	+	+
Heptageniidae			
Epeorus*	+++	+++	++
Rithrogena*	+++	++	+++
Ecdyonurus*	++	+++	+++
Heptagenia*	-	-	+
Caenidae			
Caenis	+	++	+
Baetidae	+++	+++	+++
Ephemerellidae			
Ephemerella	+	++	+
Torleya	-	+	+
Leptophlebiidae			
Habrophlebia	++	++	+
Habroleptoides	++	++	++
Paraleptophlebia	+	+	+
PLECOPTERA			
Taeniopterygidae			
Taeniopteryx*	-	-	+
Brachyptera*	++	++	++
Rhabdiopteryx*	-	+	++
Nemouridae			
Amphinemura*	++	++	++
Protonemura*	++	++	+++
Nemoura*	++	++	++
Leuctridae			
Leuctra*	+++	++	+++
Capniidae			
Capnia*	+	+	+
Capnioneura*	-	-	+
Chloroperlidae			
Chloroperla*	+	-	++
Perlodidae			
Isoperla*	++	++	++
Perlodes*	+	-	+
Perlodidae gen.*	+	-	+
Taxon	Région Jura	Jorat	Alpes
Perlidae			
Perla*	+	-	++
Dinocras*	-	-	+
ODONATA	-	+	-
HETEROPTERA	-	-	+
PLANIPENNIA			
Osmylidae			
Osmylus	+	-	+
MEGALOPTERA			
Sialidae			
Sialis	+	+	+
COLEOPTERA			
Gyrinidae	+	+	-
Dytiscidae	+	+	+
Haliplidae	+	+	+
Hydrophilidae	+	+	+
Helodidae	+	+	+
Eubridae	-	+	-
Dryopididae	-	+	-
Hydraenidae			
Hydraena	++	++	++
Ochthebius	-	-	+
Elmidae			
Elmis	++	+++	++
Esolus	++	+	+
Limnius	++	+++	++
Normandia	+	-	-
Riolus	++	++	+
Oulimnius	+	+	+
Dupophilus	-	-	+
TRICHOPTERA			
Rhyacophilidae	+++	+++	+++
Glossosomatidae*	++	+	++
Hydroptilidae*	++	++	+
Hydropsychidae	+++	+++	++
Philopotamidae	-	+	++
Polycentropidae	+	+	+
Psychomiidae	+++	++	+
Phryganeidae*	+	-	-
Limnephilidae*	+++	+++	++
Drusinae*	-	-	+
Goeridae*	+	+	+
Beraeidae*	+	-	+
Odontoceridae*	++	++	+
Sericostomatidae*	+	++	+
Lepidostomatidae*	+	+	+
Leptoceridae*	+	-	-
DIPTERA			
Blephariceridae	+	+	++
Tipulidae	++	+	++
Limonidae	+++	+++	+++
Psychodidae	++	++	++
Simuliidae	+++	+++	+++
Chironomidae	+++	+++	+++
Ceratopogonidae	++	+++	++
Stratiomyidae	+	+	+
Empididae	+++	+++	++
Dolicopodidae	+	+	+
Athericidae	++	++	+++
Dixidae	-	+	+
Anthomyidae	+	+	+
Tabanidae	+	+	-
Sciomyzidae	+	-	-

a) Identifiés d'après Tachet *et al.* (1980).

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Contribution à la connaissance de la famille Eucinetidae (Coleoptera)

Stanislav VIT
Rue de la Poterie 26, CH-1202 Genève, Suisse.

Contribution to the knowledge of Eucinetidae (Coleoptera). - A new genus, *Proeuzkus* gen. n., is described to accomodate two new species, *P. pachys* from Nepal and *P. coecus* from Thailand. *Proeuzkus pachys* sp. n. (type-species) represents the first record of a highly specialised form of Eucinetidae from the area extending from the Caucasus to Japan, while *P. coecus* sp. n. is the first anophthalmous species of the family. Another morphologically interesting species *Tohlezkus laticanthus* sp. n. is described from Malaysia, and *Eucinetus xaca* sp. n. with a highly derived aedeagus is added to the Mexican fauna.

Key-words: Coleoptera - Eucinetidae - *Proeuzkus* gen. n. - Tohlezkus - *Eucinetus* - taxonomy - new species - Nepal - Thailand - Malaysia - Mexico.

INTRODUCTION

La famille des Eucinetidae comporte actuellement six genres et 38 espèces valides, dont 28 (plus deux sous-espèces) dans le seul genre *Eucinetus* Germar, 1818. Les cinq genres restants reflètent une grande hétérogénéité de combinaisons des caractères morphologiques. Les Eucinetidae font partie des six lignées phylétiques de Coléoptères aux comportements alimentaires corrélés avec des spores. Plusieurs espèces (larves comprises) sont connues pour être associées à divers champignons et il reste admis que certaines d'entre elles sont associées à des Myxomycètes (Lawrence & Newton, 1980; Chandler, 1991). Les premières formes à morphologie buccale hautement spécialisée ont été décrites dans les genres *Tohlezkus* Vit et *Jentozkus* Vit (Vit, 1977), puis l'ensemble des données progressivement revu et remanié (Vit, 1981, 1985, 1990, 1995). Aucune hypothèse sur les relations phylogénétiques au sein de la famille n'a encore été publiée. En l'état de nos connaissances, on y soupçonne cependant une grande fréquence des caractères convergeants.

Parmi des matériaux inédits, de provenances fort diverses, souvent modestes quant au nombre d'individus disponibles, les quatre espèces réunies dans ce travail représentent des espèces porteuses de caractères intéressants ou très particuliers. Elles me semblent succeptibles d'apporter des éléments nouveaux au regard des relations phylogénétiques au sein de cette famille, où des caractères vraisemblablement dérivés se retrouvent souvent dans des groupes supposés phylétiquement éloignés.

Manuscrit accepté le 27.07.1999

Un genre nouveau, *Proeuzkus* gen. n. de la région orientale, est érigé pour inclure la première espèce hautement évoluée de la famille Eucinetidae, recensée jusqu'à présent des vastes territoires s'étendant entre l'Iran et le Japon. Deux espèces lui sont assignées; *P. pachys* sp. n., remarquable espèce du Népal (espèce-type) et le miniscule et anophtalme *P. coecus* sp. n. de la Thailande. Une curieuse espèce *Tohlezkus laticanthus* sp. n. est décrite de Malaisie et finalement une espèce du Mexique, *Eucinetus xaca* sp. n., remarquable par son édéage, complète la liste.

Abréviations utilisées:

CSV Collection S. Vit, Genève, Suisse
CUIC Cornell University, Ithaca, Etats-Unis
MHNG Muséum d'histoire naturelle, Genève, Suisse
ZML Museum of Zoology, Lund, Suède
Dans les descriptions: A.-Antennes; E.- Elytres; F.-Front; Lo.- Longueur; La. - Largeur; m. - médian(ne); P.- Pronotum; s. - sutural(e);

DESCRIPTIONS

Proeuzkus gen. n.

Espèce-type: *Proeuzkus pachys* sp. n.

Corps petit, en dessous de 1,5 mm, trapu, subglobuleux, rappelant celui des Sphaerosoma (Sphaerosomatidae); téguments pigmentés, vigoureusement ponctués et pubescents.

Tête (Fig. 1) large, encastrée dans le pronotum jusqu'au niveau des yeux, repliée normalement sur la face ventrale du corps; yeux bien développés, latéraux; insertion antennaire entièrement cachée au fond d'une profonde cavité, fermée ventralement par le bord inférieur explané de la tête, et dorsalement par l'expansion latérale du front; suture frontoclypéale fortement développée (cf. Discussion); appareil buccal (non étudié en détail) fortement modifié, probabalement du type suceur; labre court, assez peu sclérifié (comme chez *Bisaya* Reitter); palpes maxillaires quatriarticulés; palpes labiaux triarticulés, l'article apical subulé. Antennes (Fig. 7) larges, très compactes; formées de 11 articles fortement déprimés; scape asymétrique, pédicelle inséré sur sa face ventrale (comme chez *Jentozkus* Vit). Face ventrale de la tête avec de chaque côté un pli transversal caréné inexistant dans les autres genres, qui s'étend de la base du submentum jusqu'aux tempes, où il forme une protubérence dentiforme saillant latéralement en arrière des yeux. Pronotum enveloppant la base des élytres; scutellum apparent. Elytres non soudés sur la suture, sans traces de stries longitudinales, mais pourvus de 10 stries vestigiales; épipleurs entiers, faiblement élargis dans leur portion posthumérale puis progressivement atténués, méchanisme de blocage des élytres au repos présent.

Face ventrale (Figs 3-5). Processus prosternal bien développé; angle médian du mésosternum très obtus, ne formant pas de processus mésosternal; cavités mésocoxales subcontiguës; métasternum grand, ses branches latérales bien développées, non

fusionnées; épisternes métasternaux libres; épisternes et épimères mésosternaux complètement fusionnés; extrémités latérales des hanches postérieures découvertes; cinq sternites apparents chez les deux sexes; méso- et métatibias avec deux éperons apicaux chez les deux sexes. Dimorphisme sexuel limité aux seuls épérons apicaux des mésotibias.

Edéage (Figs 9-10) avec le lobe médian non tubuliforme et les paramères déplacés tout à fait dorsalement rappelle celui d'*Eucilodes* Vit.

Discussion. Le genre *Proeuzkus* est défini par son espèce-type *P. pachys* sp. n. Sa tête peu modifiée, ses yeux bien développés et l'appareil buccal du type intermédiaire rappellent *Bisaya* Reitter du Lencoran et *Eucilodes* Vit (paléarctiques), mais aussi *Euscaphurus* Casey (néarctique). Le pli transversal lamelliforme de la face ventrale de la tête, supportant ventralement les yeux, et terminé de chaque côté par une saillie dentiforme est unique chez les Eucinetidae, tout comme les antennes de ce type particulier. L'appartenance de la deuxième espèce, *P. coecus* sp. n., à ce genre, est cependant plus problématique car la tête a subi d'importantes modifications: atrophie des yeux, évolution des pièces buccales vers le type piqueur-suceur et disparition de la fosse antennaire (cf. sous *coecus*). D'autres adaptations, corrélées avec la réduction de la taille et une biologie spécialisée, sont celles déjà connues dans d'autres genres, comme *Tohlezkus* Vit ou *Jentozkus* Vit. Néanmoins, le recouvrement dorsal de l'insertion antennaire, les antennes dilatées au niveau du funicule et déprimées, le scape asymétrique et comprimé, la carène transversale de la tête (ici vestigiale et réduite à ses extrémités latérales), le mésosternum court (angle médian non lancéolé) et dépourvu de carène médiane, deux éperons apicaux des pattes, constituent les caractères communs aux deux espèces. *P. coecus* sp. n. est donc accepté ici dans le genre *Proeuzkus* en tant que son espèce dérivée.

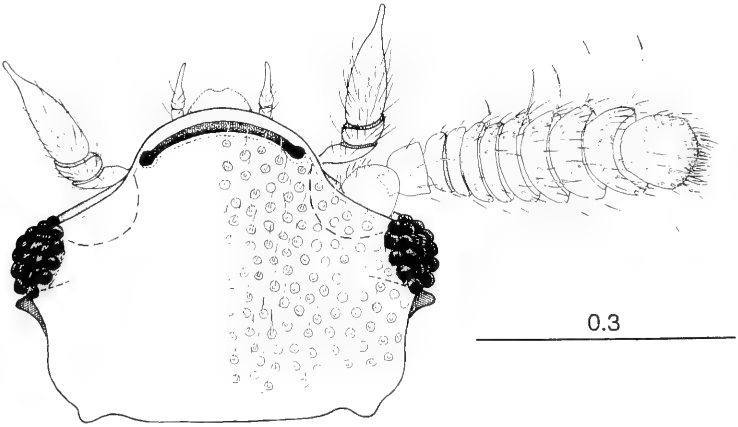
Proeuzkus pachys sp. n. Figs 1, 3-11

Matériel. Holotype ♂, étiqueté: NEPAL, Khandbari District, above Tashigaon, 3100 m 7.IV.1982, A. & Z. Smetana. (MHNG); Paratypes: 2♂, mêmes données que l'holotype, (1♂ disséqué et conservé en glycérine). (MHNG); 1♂, 1♀ idem HT, "Bakan" W of Tashigaon 3200 m, 5.IV.1982, A. & Z. Smetana. (MHNG, 1♀ CSV).

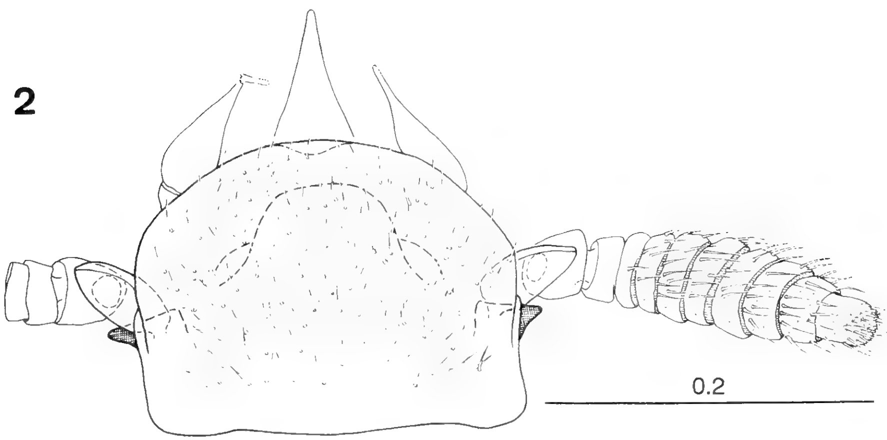
Espèce aptère chez les deux sexes, coloration d'un brun foncé rougeâtre, pattes à peine plus jaunâtres; pubescence courte, couchée; téguments non translucides, brillants, entièrement densément et fortement ponctués. Corps fortement convexe, trapu, acuminé apicalement. Longueur 1,40-1,45 mm, largeur 0,97-1,02 mm, située en avant du milieu du corps.

Tête (Fig. 1). Large, faiblement convexe, retrécissant en arrière des yeux et convergeant en arrière; tempes doublées ventralement, en arrière des yeux, par l'extrémité latérale dentiforme de la carène ventrale transversale de la tête; largeur de la tête (yeux compris) d'un tiers supérieure à sa longueur médiane (labre non compris), cette dernière subégale à la largeur du front. Yeux saillants latéralement et parfaitement isolés de la face ventrale de la tête, composés d'une vingtaine de grosses ommatidies, rebordés en bas par une fine carène subocculaire indistincte en vue dorsale. Côtés explanés du front faiblement sinueux au-dessus de l'insertion antennaire, cette dernière

1



2

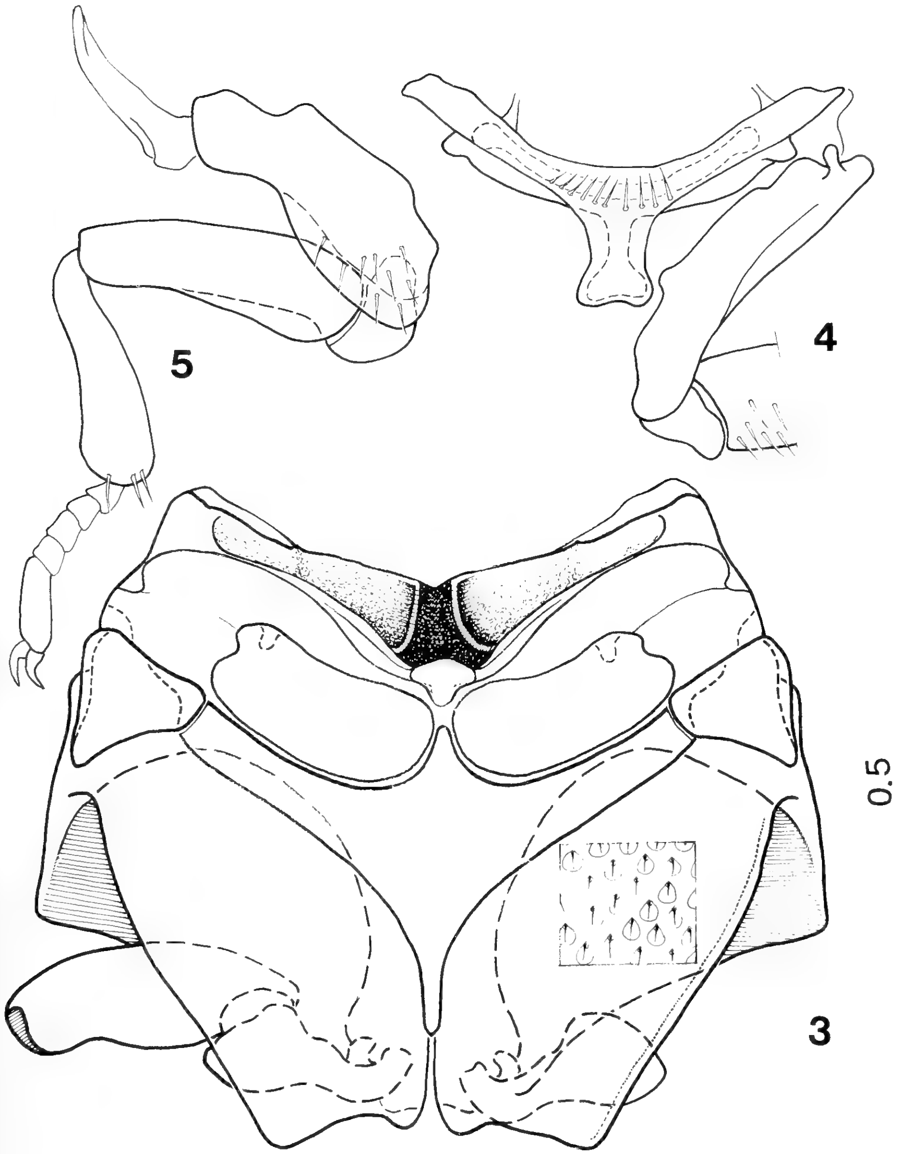


Figs 1-2

Proeuzkus spp. 1, *P. pachys* sp. n.: tête, vue dorsale; 2, *P. coecus* sp. n.: tête, vue dorsale. Mesures données en mm.

entièrement cachée au fond d'une profonde fosse antennaire entièrement fermée; frontoclypéus court, amplement arrondi en avant, les côtés faiblement rebordés; suture frontoclypéale fortement développée, formant un canal profond (qui semble en partie invaginé), terminé de chaque côté par une fossette circulaire (cf. Discussion). Appareil buccal (Fig. 6) du type spécialisé; mandibules et maxilles indistinctes; labre petit, ramassé, peu sclérifié; dernier article des palpes maxillaires grand, étiré en pointe, l'apex prolongé par une courte épine hyaline; palpes maxillaires triarticulés, très petits, dépassant à peine sur le côté.

Antennes (Fig. 7) compactes, courtes (à peine aussi longues que la moitié de la largeur basale du pronotum), fortement déprimées, très larges (seulement trois fois plus longues que larges), leur plus grande largeur située au niveau du 8ème segment; articles



FIGS 3-5

Proeuzkus pachys sp. n. face ventrale du corps: 3, hanches postérieures, méta - et mésosternum (pattes omises); 4, prosternum; 5, patte antérieure. (Mesures données en mm).

fermement encastrés les uns dans les autres, portant de très longues soies semi-dressées. Scape en grande partie visible, ovoïde, asymétrique, protubérant à son bord distal et cachant partiellement le pédicelle; ce dernier subcylindrique, aussi long que large, inséré sur la face ventrale du scape; articles 3-7 du funicule très courts, fortement transverses (au moins 3 fois plus larges que longs); articles 9 et 10 plus robustes, transverses, deux fois plus larges que longs, (évoquant une massue mal différenciée); segment apical subovoïde, plus large que long, surmonté d'une pubescence apicale.

Pronotum très grand, occupant un quart de la longueur totale de l'animal. Base doublement sinueuse mais peu projetée en arrière; scutellum grand, triangulaire, entièrement visible; côtés finement rebordés; angles postérieurs aigus, enveloppant la base des élytres. Ponctuation forte, plus espacée que celle de la tête ou celle des élytres.

Elytres sub-hémisphériques, aussi longs que larges ensemble; côtés fortement arqués; suture élytrale non soudée; strie juxtasuturale présente, raccourcie, marquée tout au plus dans la moitié apicale; interstrie juxtasutural renflé dans le tiers apical. Ponctuation grossière et dense, non alignée en stries longitudinales; dix stries ponctuées demeurent cependant nettement distinctes sur chaque élytre en milieu aqueux, les stries 2 et 4 raccourcies, ne dépassant pas le tiers basal.

Face ventrale (Figs 3-5) brillante et aussi fortement ponctuée que la face dorsale, aire médiane faiblement déprimée. Epipleures entiers, faiblement élargis dans leur portion posthumérale, puis longuement atténués. Limite médiane du mésosternum simplement obtuse, angle apical renflé, glabre, non étiré en un processu médian séparant les hanches; métasternum grand, sutures transverses et suture médiane indistinctes; languette métasternale bien développée, courte, subparallèle; metépisternes trapus, subtriangulaires (comme chez *Eucinetus apterus* Vit, 1990), le bord externe explané, formant un dispositif de blocage des élytres; mesépimères transverses, fusionnés avec les mesépisternes, la suture indistincte, leur structure tégumentaire cependant différenciée. Plaques coxales larges, mais orientées longitudinalement, laissant les extrémités latérales glabres des hanches postérieures largement découvertes; bords latéraux rebordés, arqués puis discrètement sinués avant les angles apico-externes; ces derniers presque droits, émoussés, peu saillants en arrière, n'atteignant cependant pas le bord postérieur du premier segment abdominal; bords postérieurs faiblement concaves et pourvus d'une nette encoche proche de la ligne médiane; premier segment abdominal pourvu d'une courte carène médiane; le 5ème rebordé; sternites 6 et 7 faiblement sclérifiés, rétractés au repos à l'intérieur de l'abdomen.

Pattes (tarses compris) peu modifiées, les tibias subcylindriques, s'élargissant progressivement vers l'apex. Fémur de la patte antérieure (Fig. 5) simple, plus long que le tibia, ce dernier plus long que le tarse; protarses sans dimorphisme sexuel; les deux éperons apicaux du protibia petits, pratiquement indistincts; mésotibia faiblement recourbé, armé sur sa face externe de nombreuses (12-15) épines plus fortement pigmentées; apex avec deux éperons de longueur subégale chez les deux sexes; éperon externe fortement modifié chez le mâle (Fig. 8); métatibia coudé à la base, aussi long que le tarse, face externe couverte de 12-15 épines effilées et plus fortement pigmentées, non scindées en deux groupes distincts; apex avec deux éperons dont le plus grand

atteint la base du peigne apical du segment basal du tarse; ce dernier subégal aux articles 2, 3, 4 ou 3, 4 et 5 réunis.

Edéage (Figs 9, 10) avec le lobe médian très large, simplement lamelliforme, dépourvu de renflure apicale; paramères amplement arrondis apicalement, très rapprochés dorsalement. Ce type d'édéage présente quelques analogies avec celui d'*Eucilodes* Vit (Vit, 1977, 1985).

Biologie inconnue, mais il s'agit d'une espèce récoltée au-dessus de 3000 m.

Distribution. Connu seulement de la localité-type: Népal, Kandbari district.

Discussion. Le caractère externe le plus frappant de *P. pachys* sp. n. est l'aspect du tégument: épais, brillant, il est vigoureusement ponctué et exempt de microréticulations et de ponctuation nettement râpeuse. Or la ponctuation franche et grosse n'est connue que chez de grandes espèces ailées (*Eucinetus* Germar, *Nycteus* Latreille, *Eucilodes* Vit, *Euscaphurus* Casey), où elle est confinée à la face dorsale de la tête. Chez *P. pachys* elle s'étend, presque identique, sur l'ensemble de la face dorsale et ventrale du corps.

Quant à la conformation de la suture frontoclypéale, formant une sorte de gouttière invaginée, flanquée de chaque côté d'une fossette, elle demeure également unique. Sa présence est d'autant plus surprenante qu'on relève, chez les Eucinetidae, une tendance certaine à la disparition de la suture frontoclypéale chez toutes les petites espèces (y compris *Bisaya nossidiiformis* Reitter) présentant un appareil buccal du type modifié. Il pourrait s'agir d'un dispositif rudimenraire du type mycangium (Crowson, 1981), destiné au transport des spores de champignons (notamment Myxomycètes), dont des Eucinetidae sont supposés se nourrir. Cependant des données attestées, concernant les particularités alimentaires des Eucinetidae, restent encore trop pauvres (Lawrence & Newton, 1980; Chandler, 1991).

Proeuzkus coecus sp. n. Fig. 2

Matériel. Holotype ♀, étiqueté: Thailand Doi Inthanon 1750 m. 7.XI.85 Löbl, Burckhardt. (MHNG); Paratype. 1♀, étiqueté: /Thailand-Chiang Mai Doi Saket "1130 m. 4.XII. 87" P. Schwendinger. (MHNG - exemplaire disséqué conservé en glycérine).

Espèce aptère et anophtalme (femelle), coloration entièrement d'un jaune clair translucide, épines latérales et cils apicaux des tibias et des tarses fortement rembrunis, noirâtres; pubescence des téguments fine, couchée. Corps trapu, une fois et demie plus longue que large, régulièrement convexe, peu atténué apicalement. Longueur 0,86 mm, largeur 0,55 mm, située au niveau posthuméral.

Tête (Fig. 2). Large (une fois et demie plus large que longue sur la ligne médiane, labre non compris), modérément convexe, parallèle au niveau des tempes et presque semi-circulaire en avant; tempes doublées ventralement, en dessous de l'insertion antennaire, par une lame latérale dentiforme non prolongée ventralement sous forme d'une carène transversale de la tête. Yeux absents; côtés du front fortement explanés en avant de l'insertion antennaire; fosses antennaires nulles car non fermées ventralement par le bord inférieur explané de la tête, développé chez d'autres espèces. Appareil buccal du type piqueur-suceur; suture frontoclypéale absente; clypéus amplement arrondi, échancré au milieu, finement rebordé; ponctuation forte, éparse, granuleuse.

Antennes compactes, déprimées, courtes (plus courtes que la moitié de la largeur basale du pronotum), larges (seulement quatre fois plus longues que larges), leur plus grande largeur située à peu près au niveau du 8ème segment; articles fermement encastrés les uns aux autres. Scape visible dorsalement, fortement comprimé, étroit, allongé, et protubérant à son bord distal, cachant pariellement le pédicelle; ce dernier robuste, subcylindrique,inséré sur la face ventrale du scape; articles 3 à 7 du funicule fortement transverses (deux à trois fois plus larges que longs); articles 8 à 10 plus allongés, évoquant une massue mal différenciée; segment apical réduit, subovoïde, plus long que large, surmonté d'une pubescence apicale.

Base du pronotum doublement sinueuse, fortement projetée en arrière, suplombant celle des élytres; scutellum grand mais entièrement caché sous le rebord basal du pronotum; côtés droits, finement rebordés; angles postérieurs aïgus, étirés en arrière. Ponctuation fine et éparse sur le disque, plus grossière dans les déclivités latérales.

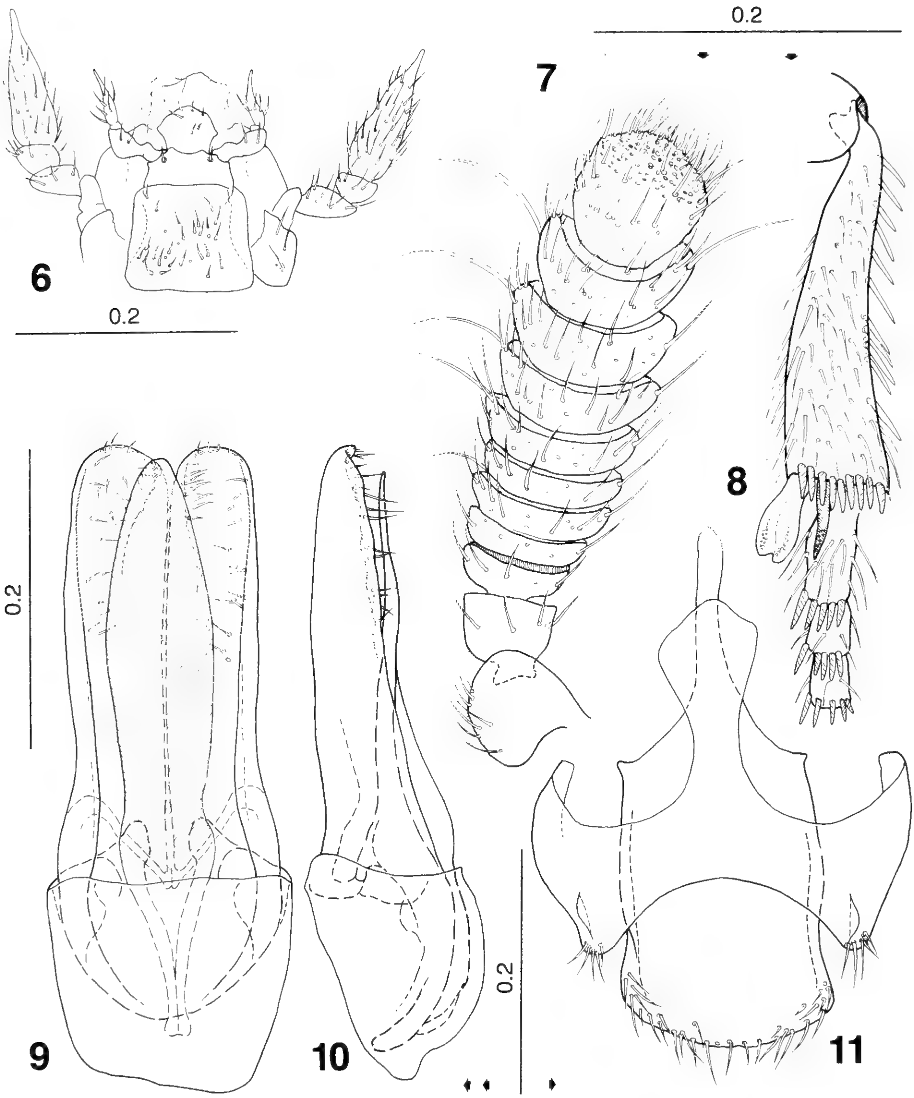
Elytres d'un tiers plus longs que larges ensemble; côtés arqués, acuminés vers l'apex; suture élytrale non soudée; strie juxtasuturale et stries longitudinales absentes; six stries vestigiales, rudimentaires et incomplètes demeurent néanmoins perceptibles lors d'un examen de l'élytre dans une solution aqueuse.

Face ventrale avec une forte ponctuation serrée sur les plaques coxales et le métasternum; aire médiane des plaques coxales à peine déprimée.

Epipleures entiers, étroits, atténués à l'apex. Hanches médianes contigües; limite médiane du mésosternum obtuse, angle apical renflé, glabre, non étiré en un processus médian séparant les hanches; métasternum petit; languette médiane longuement effilée, se prolongeant jusqu'au bord postérieur des plaques coxales sous forme d'une fine carène médiane; branches latérales étroites, entièrement fusionnées avec les métépisternes; dispositif de blocage des élytres présent; mésépimères fusionnés avec les mésépisternes. Plaques coxales larges mais orientées longitudinalement, laissant découvertes les extrémités latérales glabres des hanches postérieures; bords latéraux délicatement rebordés, faiblement arqués; angles apico-externes aigus, projetés en arrière, au-dessus du bord postérieur du premier segment abdominal; bords postérieurs doublement sinueux. Cinq sternites visibles chez la femelle, le cinquième large, ogival, très finement rebordé, aussi long que les sternites 3 et 4 réunis.

Pattes (tarses compris) très robustes, les tibias déprimés, s'élargissant fortement vers l'apex. Protibia aussi long que le tarse, apex sans éperons apicaux distincts; fémurs des pattes antérieures et médianes avec une saillie dentiforme contigüe au trochanter; face externe du mésotibia avec deux rangées longitudinales, serrées, de soies spiniformes plus pigmentées; apex avec deux éperons effilés; métatibia aussi long que le tarse, face externe du métatibia garni de nombreuses soies spiniformes rembrunies, formant un groupe préapical plus ou moins nettement séparé, apex avec deux éperons effilés plus longs que le segment basal du tarse; ce dernier plus court que les articles 2, 3, 4 ou 3, 4 et 5 réunis.

Distribution. Les deux captures proviennent de la province de Chiang Mai au nord de la Thailande, de tamisages de débris végétaux en forêt de montagne, entre 1200 et 1700 m.



FIGS 6-11

Proeuzkus pachys sp. n. : 6, appareil buccal, vue ventrale; 7, antenne; 8 mésotibia et les éperons apicaux (♂); 9, édéage, vue ventrale; 10, édéage, vue latérale; 11, segments abdominaux VI et VII (♂). (Mesures données en mm).

Discussion. L' anophtalmie de cette espèce et la présence d'un puissant appareil buccal du type piqueur-suceur ont pour corollaire de très notables modifications dans la morphologie de la tête: de longues tempes parallèles; bords latéraux du front très fortement explanés; échancrure gulaire occupant pratiquement toute la face ventrale de la tête, d'où la suppression du pli transverse de la tête, dont il ne subsiste que les extrémités latérales dentiformes; absence du bord latéral inférieur de la tête qui normalement constitue la paroi ventrale de la fosse antennaire. D'autres modifications à caractère convergent, que l'on retrouve chez d'autres espèces et genres de la famille: fusion des pièces sternales, absence de la strie juxtasuturale, réduction des stries élytrales ou réduction du nombre de sternites apparents, sont à mettre en corrélation avec la réduction notable du corps (0,86 mm = la plus petite espèce connue). Il serait utile de pouvoir connaître le mâle et la structure de l'édéage de cette espèce.

Tohlezkus laticanthus sp. n. Figs 12-16

Matériel. Holotype ♂, étiqueté: MALAYSIA: Pahang, 4 mi NE Cameron Highlands, 23-25.IV. 1977, (berlese leaf litter), L. Watrous. (CUIC).

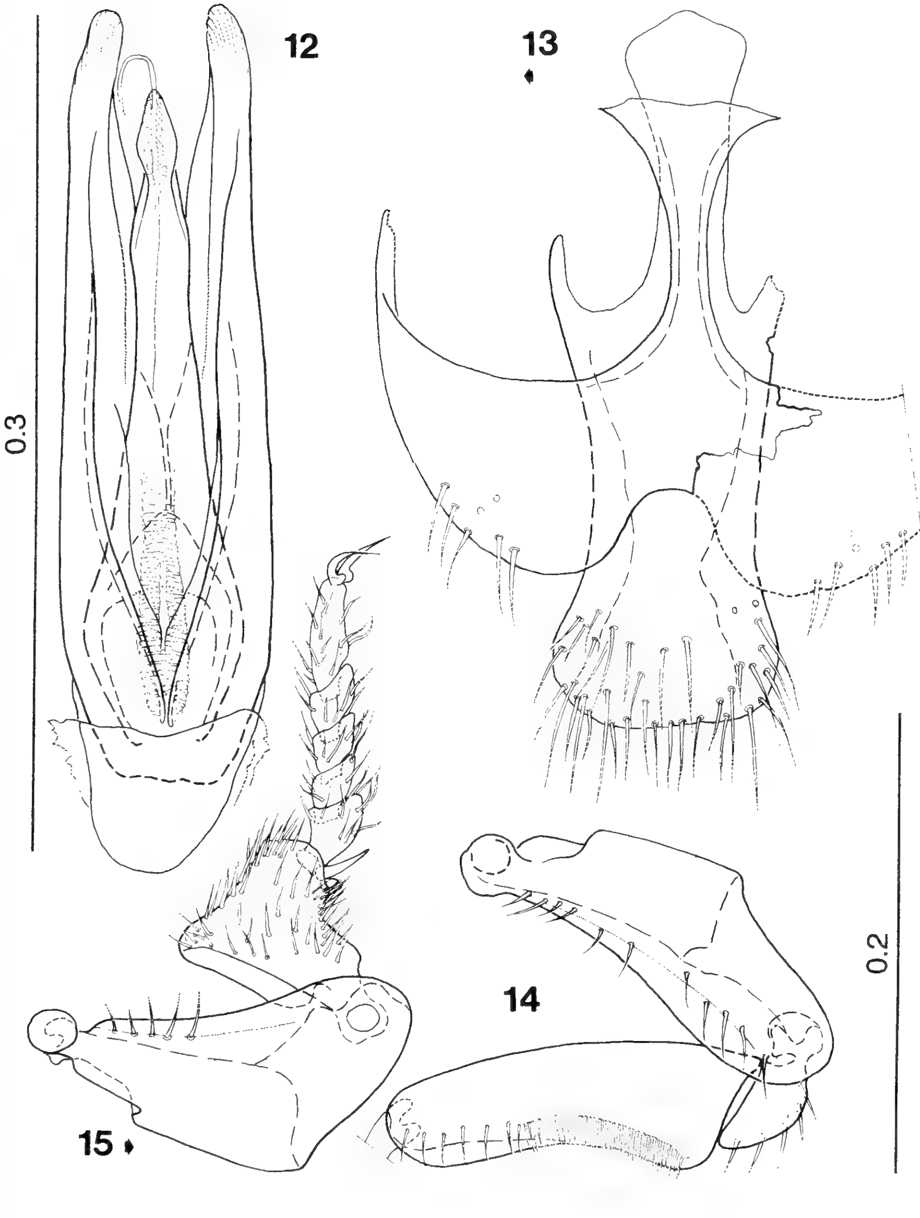
Espèce aptère (pas d'ailes distinctes par transparence des téguments chez le mâle), coloration entièrement d'un brun roussâtre clair, côtés de la tête rembrunnis, cils apicaux des tibias et des tarses à peine plus foncés; pubescence fine, couchée. Corps allongé, deux fois plus long que large, faiblement acuminé apicalement. Longueur 1,05 mm, largeur 0,62 mm, située au niveau posthuméral.

Tête. Large, subogivale, modérement convexe, parallèle au niveau des tempes; côtés convergeant en avant; clypéus arrondi; ponctuation forte, subrâpeuse. Yeux bien développés, latéraux, formés d'un gros grain hyalin fortement saillant latéralement; limites latérales du cranium fortement pigmentées; insertion antennaire entièrement cachée sous le bord explané du front; cavité antennaire fermée ventralement. Appareil buccal du type piqueur-suceur; suture frontoclypéale absente; bord antérieur rebordé.

Antennes compactes, peu déprimées, un peu plus longues que la moitié de la largeur basale du pronotum, épaisses, au moins 5 fois plus longues que larges, leur plus grande largeur située au niveau du 8ème segment; articles encastrés les uns dans les autres. Scape en partie caché sous le rebord explané du front, cylindrique; pédicelle cylindrique, subcarré, inséré axiallement; articles 3 à 6 du funicule courts, transverses (deux fois plus larges que longs); articles 7 à 11 plus robustes, plus allongés, faiblement transverses; segment apical grand, subovalaire, plus long que large, surmonté de pubescence apicale.

Base du pronotum doublement sinueuse, projetée en arrière, suplombant la base des élytres; scutellum petit, entièrement caché; côtés très finement rebordés; angles postérieurs aïgus, étirés en arrière. Ponctuation nette sur le disque, plus grossière dans les déclivités latérales.

Elytres une fois et demie plus longs que larges ensemble, ratio Lo.s./La. = 1,46; côtés peu arqués, subparallèles, faiblement acuminés; vraisemblablement soudés sur la suture; strie juxtasuturale oblitérée; stries longitudinales absentes; cinq stries ponctuées vestigiales et incomplètes cependant perceptibles dans la portion basale lors d'un



FIGS 12-15

Tohlezkus laticanthus sp. n.: 12, édéage, vue ventrale; 13, segments abdominaux VI et VII (£); 14, hanche antérieure et profémur (normalement constitués); 15, patte antérieure gauche (tératologique). Mesures données en mm.

examen dans une solution aqueuse. Ponctuation très serrée et subrâpeuse, arrangée, près de la base, partiellement, en paliers transverses .

Face ventrale entièrement, densément, et râpeusement ponctuée; aire médiane des plaques coxales nettement déprimée.

Epipleures entiers mais de forme particulière: d'abord étroits et fortement comprimés dans leur portion post-humérale, puis larges, s'élargissant même progressivement jusqu'au niveau du troisième sternite et brièvement atténués vers les angles suturaux. Processus mésosternal semblable à celui rencontré par exemple chez *Euscaphurus spinipes* Vit; élancé, cordiforme, pourvu d'une carène médiane, acuminé apicalement, mais ne séparant pas les hanches médianes; cavités cotyloïdes contiguës. Métasternum petit; languette médiane fortement éffilée, se prolongeant jusqu'au bord postérieur des plaques coxales sous forme d'une fine carène médiane; branches latérales étroites, tout au plus faiblement élargies à leurs extrémités latérales; entièrement fusionnés avec les métépisternes; mésépimères, fortement transverses, subfusionnés, leur suture avec le mesépisterne distincte; mésosternum et mésépisternes fusionnés. Plaques coxales orientées longitudinalement, étroites, laissant largement découvertes les extrémités latérales glabres des hanches postérieures; bords latéraux délicatement rebordés, faiblement arqués; angles apico-externes aigus, émoussés au sommet, fortement projetés en arrière au-delà du bord postérieur du premier sternite; bords postérieurs fortement convergents vers la ligne médiane. Cinq sternites visibles (sûrement chez les deux sexes), le cinquième large, ogival, finement rebordé, aussi long que les sternites 3 et 4 réunis. Chez le mâle les sternites 6 et 7 (Fig. 13) restent faiblement sclérifiés et entièrement retractés dans l'abdomen.

Pattes (tarses compris) robustes, déprimées, tibias s'élargissant fortement vers l'apex; profémur (Fig. 14) avec une saillie dentiforme contigüe au trochanter et un peigne de soies longeant le bord externe; patte tératologique (cf. Remarque) de cette exemplaire (Fig. 15) présente un éperon apical et le protarse non dilatés chez le mâle (!); mésotibia faiblement incurvé, plus court que le tarse; face externe avec deux rangées longitudinales serrées de soies spiniformes, rembrunies, apex avec deux éperons dont l'interne fortement développé chez le mâle, épais, incurvé et renflé apicalement, presque aussi long que le segment basal du tarse; métatibia faiblement incurvé, aussi long que le tarse; face externe garnie de nombreuses soies spiniformes plus pigmentées et d'un peigne préapical d'épines foncées, apex avec deux éperons dont un remarquablement développé, en forme de "chausse-pied" (Fig. 16), dilaté, spatuliforme, tronqué apicalement, plus long que le segment basal du tarse; ce dernier subégal aux segments 2, 3, 4 ou 3, 4 et 5 réunis.

Edéage (Fig.12) pourvu de structures membraneuses internes et de paramères explanés du côté dorsal et finement ciliés à l'apex.

Caractères sexuels. Un seul mâle étant connu, il n'est pas possible de définir si l'éperon apical modifié des métatibia (Fig.16) est, ou n'est pas, un caractère sexuel du mâle (au même titre que celui des mesotibias), ou un caractère propre de cette espèce.

Remarque. Les pattes antérieures de cet exemplaire unique sont incomplètes (Figs 14-15). A l'une manque le tibia, l'autre est sujette à une malformation curieuse, où son tibia, de surcroît malformé, est articulé directement avec la hanche.

Discussion. Les deux caractères remarquables de cette espèce sont ses épipleures dilatés dans la partie subapicale et l'hypertrophie de l'éperon apical des métatibias. On relève néanmoins, ou niveau de la famille, plutôt une tendance à la réduction des épipleurs et une régression des éperons apicaux des tibias.

Eucinetus xaca sp. n. Figs 17-20

Matériel. Holotype ♂, étiqueté: Mexico: Oaxaca, 12 km N Oaxaca City, hwy 175 1900 m. 28.IX. 1990, sifting litter at small stream, tropical mountane forest. (ZML). Paratypes. 2♀♀ mêmes données que l'holotype; 1♂ (1.X. 1990), 2♀♀ (5.X. et 8.X.1990) Mexico: Oaxaca, 12 km N Oaxaca City, hwy 175 1900 m. 1.-8.X.1990 leg. R. Raranowski, Pit-fall traps near small stream, trop. mount. forest. (ZML); 2♂♂, 2♀♀ Mexico: Oaxaca 12 km N Oaxaca 2000 m., 15.IX.1986 R. Baranowsk, sifting litter in creek, trop. mont. forest; 2♂♂, 2♀♀ Mexico: Oaxaca 10 km. N Oaxaca 1900 m. 13.IX. 1986 R. Baranowski, sifting litter at small stream, trop.mont. forest. (ZML, CSV). Autres. 1♀ (*xaca* ?) Jalisco 50 km S Puerto Vallarta 800 m. 16.VI.1986 leg. M. Sörensson & B. Mårtensson (ZML).

Longueur dorsale médiane (tête non comprise) 3,1-3,6 mm, corps subparallèle, la plus grande largeur 1,73-1,86 mm; ratio Lo.m. (sans tête)/ La. = 1,97-2,01 Coloration presque uniforme, d'un brun rougeâtre foncé, brillant, partie apicale des élytres parfois sombre; pattes plus claires; antennes tricolores, claires et noirâtres.

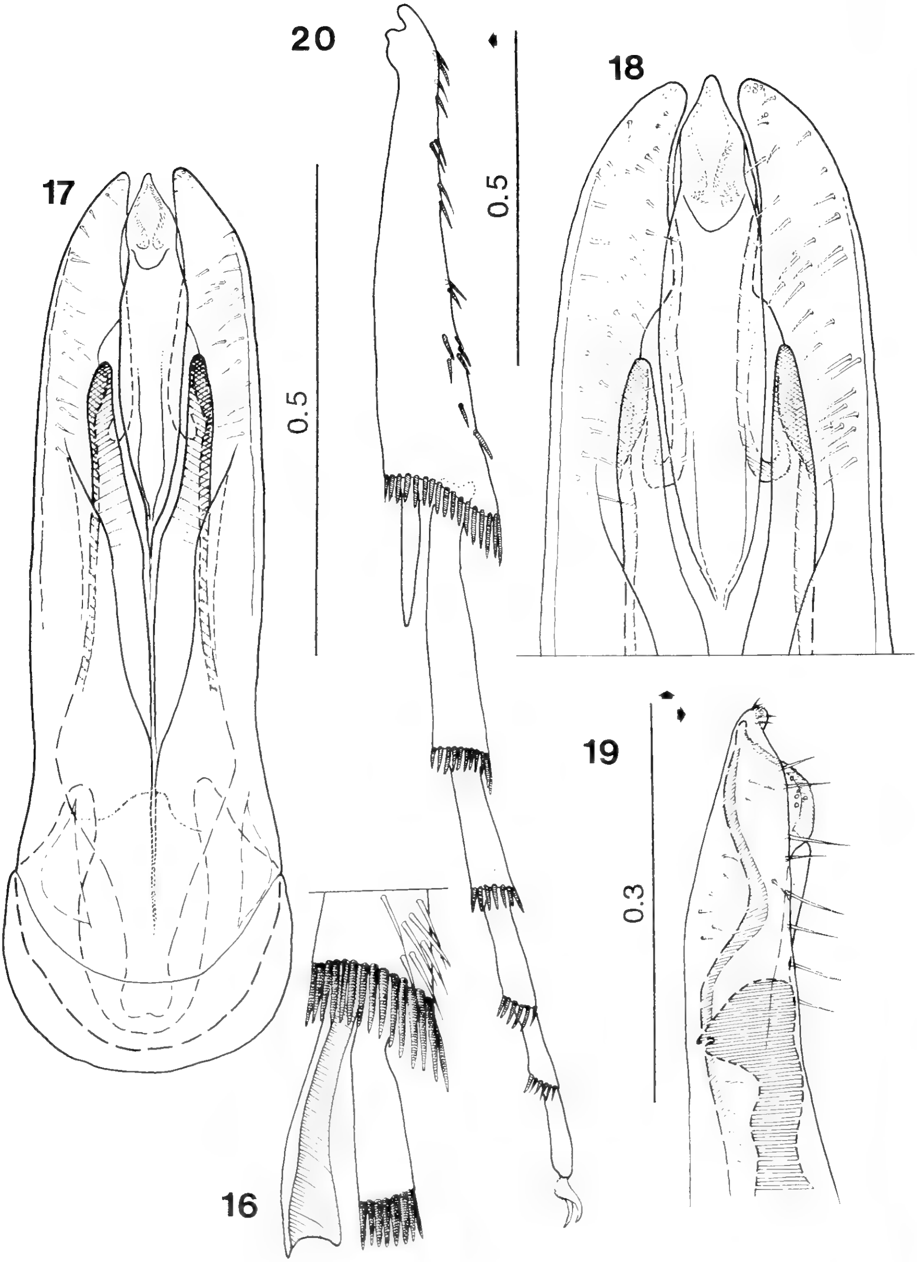
Tête. Transverse, longueur médiane inférieure à la largeur du front entre les yeux, ratio Lo.m./La.F. = 0,83-0,92; ponctuation fine, serrée.

Antennes tricolores (articles 1-3 bruns, 4-9 noirâtres, 10 et 11 jaunâtres), longues environ comme la base du pronotum mesurée en vue dorsale, ratio Lo.A./La.P. = 0,95-1,11; tous les articles allongés; pédicelle trois fois plus long que large, plus long que le 3ème; ce dernier grêle, tout juste plus court que le 4ème; articles 4 à 10 subégaux, diminuant progressivement en longueur; 11ème article une fois et demie plus long que large.

Ponctuation du pronotum fine et serrée sur le disque, aussi forte que celle de la tête dans les déclivités latérales.

Elytres longuement subparallèles, ratio Lo.m./La.(sexes confondus) = 1,1,60-1,74, rebord latéral perceptible de dessus au moins dans le tiers apical. Strie juxtasuturale oblitérée à environ trois longueurs de scutellum de la base; interstrie juxtasuturale faiblement enflé à l'apex; stries longitudinales seulement peu visibles, marquées tout au plus dans la moitié apicale, interstries à peine convexes; ponctuation fine, paliers transverses très serrés (4 paliers = 0,1 mm).

Face ventrale. Epipleures raccourcis, se confondant avec le bord de l'élytre au niveau du 4e sternite; leur largeur après l'étranglement posthuméral égale à la moitié de la longueur du 3ème article antennaire. Métasternum densément ponctué; languette métasternale longue, subtriangulaire, suture médiane nettement imprimée; sutures transverses distinctes. Mesurés sur leur bords externes, les métépisternes sont aussi longs que les mésépimères, ces derniers presque aussi larges que longs; suture séparant les mésépimères des mésépisternes nette, non renflée. Plaques coxales larges, transversales, cachant parfaitement les extrémités latérales des hanches postérieures; côtés non rebordés; angles apico-externes arrondis (atteignant le niveau du bord postérieur du premier segment abdominal); bords postérieurs simples, convergeant vers la ligne médiane. Bord postérieur du 5e et 6e sternite amplement échancré (♂).



FIGS 16-20

Tohlezkus laticanthus sp. n.: 16, éperon apical des métatibias; *Eucinetus xaca* sp. n.; 17, édéage, vue ventrale; 18, édéage, détail de la partie apicale du lobe médian; 19, édéage, vue latéral du même; 20, patte postérieure, tibia et tarse. Mesures données en mm.

Patte antérieure.Tarse fortement dilaté chez le mâle; subégal chez les deux sexes à la longueur du tibia, ce dernier modérément renflé chez le mâle, subparallèle chez la femelle.

Patte médiane. Tibia très nettement plus court que le tarse, progressivement élargi, bord externe avec 3 à 8 épines noires, couchées, apex avec un seul éperon peu développé chez la femelle, deux éperons de longueur subégale chez le mâle, l'éperon interne simplement épaissi.

Patte postérieure (Fig. 20). Tibia nettement plus court que le tarse, légèrement incurvé, garni sur sa face externe de 13 - 20 épines semi-dressées, plus 2 - 4 épines dans le groupe pré-apical pas nettement singularisé; un seul éperon apical, aussi long que la moitié du basitatarse; longueur de ce dernier nettement inférieure à celle des articles 2, 3, 4 ou 3, 4 et 5 réunis.

Edéage (Figs 17-19) pourvu de puissantes excroissances dentiformes à la base de l'étranglement subapical du lobe médian, portion distale des paramères lamelliforme (cf. Discussion).

Distribution. Mexique méridional, Oaxaca.

Discussion. Avec d'importantes modifications de la portion apicale des paramères (normalement arrondie) et de la portion subapicale du lobe médian (normalement tubuliforme), muni ici de puissantes excroissances latérales fortement sclérifiées, l'édéage de *Eucinetus xaca* sp. n. confirme une évolution morphologique tout à fait intéressante. Ce type d'édéage a déjà été signalé (Vit, 1990) pour deux autres espèces du groupe *haemorrhoidalis*, à savoir: *E. pecki* Vit et *E. apterus* Vit, décrites également du Mexique. Or cette évolution vers une forme différente de l'édéage - pour l'instant parfaitement isolée au sein du genre *Eucinetus* - apparaît chez des espèces mexicaines de façon tout à fait endémique. Elle ne se rencontre ni au nord, chez les espèces néarctiques, ni au sud, chez celles néotropicales. L'édéage d'*E. xaca* sp. n. est très proche du celui d'*E. apterus*, l'unique espèce aptère du groupe *haemorrhoidalis*, bien caractérisée par ailleurs par une réduction des métépisternes, relative à la disparition des ailes métathoraciques.

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Spatio-temporal distribution of size classes and larval instars of aquatic insects (Ephemeroptera, Trichoptera and Lepidoptera) in a *Potamogeton pectinatus* L. bed (Lake Geneva, Switzerland)

Ruth BÄNZIGER
Laboratoire d'écologie et de biologie aquatique, 18 ch. des Clochettes,
University of Geneva, CH-1206 Geneva, Switzerland.

Spatio-temporal distribution of size classes and larval instars of aquatic insects in a *Potamogeton pectinatus* L. bed (Lake Geneva, Switzerland). - Temporal changes of aquatic insect instars or size classes were monitored in different parts of a *Potamogeton pectinatus* bed. The hypothesis of a different distribution of the aquatic insects in the macrophyte bed according to their life stage and of a spatio-temporal segregation of congeneric species was tested. Head capsules widths of seven insect species (*Caenis horaria* and *C. luctuosa* (Ephemeroptera), *Mystacides azurea*, *M. longicornis*, *Oecetis lacustris* and *O. ochracea* (Trichoptera) and *Acentria ephemerella* (Lepidoptera)) were measured at monthly intervals from May to November 1994. Samples were taken in the edge and in the centre of the macrophyte bed on all sampling occasions, and in May, June and July, additional samples were taken from the 2 m sediment belt adjacent to the macrophyte bed. Each couple of congeneric species showed segregation by size before hibernation and showed delayed emergence patterns.

Key-words: Lake - Ephemeroptera - Trichoptera - Lepidoptera - macrophyte - distribution - size class.

INTRODUCTION

Habitat segregation or space partitioning among closely related species have been often addressed in rivers (Malas & Wallace, 1977; McAuliffe, 1984). Few papers, however, have been concerned with this subject in lakes. Species with similar ecological niches are not always separated in space and time, thus competition is not necessarily involved and some congeneric species do coexist (Hildrew & Edington, 1979). Segregation, if there is any, is therefore likely to occur at another scale than at the species level. In larval insects or nymphs, delayed growth of the last instars or nymphal stages have been observed, often resulting in temporal segregation of emergence (Macan, 1965; Tudorancea & Green, 1975; Malas & Wallace, 1977; Bengtsson, 1981; Sweeney & Vannote, 1981; Brittain, 1982). Hildrew & Edington (1979) showed that two congeneric hydropsychid caddisflies avoided coexistence by different microhabitat colonization of some instars. Hydropsychidae were also studied

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by Muotka (1990) who showed them having different microhabitat preferences according to different larval stages. Minshall (1984) observed changes in spatial distribution of insects according to developmental stages. Altogether, between egg and adult, the growing insects may live through many different feeding modes, behaviour or habitat niches (Winterbourn, 1971; Resh, 1979; Palmer *et al.*, 1993). These changes according to development allow them to reduce competition if resources are scarce.

In a previous paper (Bänziger *et al.*, subm.), we demonstrated differences in densities of several invertebrate taxa between the edge and the centre of macrophyte beds. The question arose whether these differences in density could be related to larval instar or size class distribution.

The purpose of the present study was to test the following hypotheses in a *Potamogeton pectinatus* L. bed of the littoral zone of Lake Geneva: i) distribution of insects in macrophyte beds changes according to larval instar or size class; and ii) congeneric species living in the same macrophyte bed differ in size and/or timing of larval instars.

MATERIAL AND METHODS

The samples were taken in a *Potamogeton pectinatus* L. bed near Corsier (46°16' N, 6°12' E) in the littoral zone of Lake Geneva, Switzerland.

Samples were taken by scuba diving at a depth of 3.0 - 3.5 m in the edge, in the centre and adjacent to the macrophyte bed. The edge was defined as the margin of the bed characterised by lower macrophyte stem density, the presence of more filamentous algae (depending on the season) and by shorter shoots than in the centre of the bed. This corresponded to the 2 m wide outer belt of the macrophyte bed. Macrophyte density in the centre of the bed was 80 stems m^{-2} at maximum density, i.e. in July. The (arbitrarily) 2 m wide area around the macrophyte bed, consisting of sediment, was defined as the adjacent sediment.

Macrophyte samples were taken from May through to November 1994, adjacent sediment was sampled from May to July. When the macrophytes senesced - from October to November - sampling was carried on in the plant underlying sediments and the remains of the *Potamogeton* bed. Collections were made using different sampling gears depending on the substrate:

Collections of fully grown macrophytes were made using a sampler modified after Gerking (1957) with a surface area of 0.25 m^2 and a height of 1 m. When vegetation was less dense a frame of 0.0625 m^2 with an attached net was used. Each of the two sampling gears was lifted down on the macrophytes by a scuba diver, the plants were teamed out of the sediment and the sampler was closed: the Gerking-like sampler by a trap and the net by a string.

Sediments underlying the macrophyte bed were collected using corers covering an area of 0.005 m^2 and pushed 10 cm deep into the sediments. Adjacent sediments were collected inside a 0.25 m^2 frame using the same net as for vegetation samples.

In the laboratory, samples were thoroughly rinsed with tap water and the macroinvertebrates were retained in a 250 μm sieve. They were conserved in 4% formalin.

Seven insect species were retained for measurements: *Caenis horaria* (L.), *C. luctuosa* (Burm.) (Ephemeroptera), *Mystacides azurea* (L.), *M. longicornis* (L.), *Oecetis lacustris* (Pictet), *O. ochracea* (Curtis) (Trichoptera) and *Acentria ephemerella* (Denis and Schiffermüll.) (Lepidoptera) on the basis of their abundance in the samples, their identification and/or the availability of congeneric species.

Larvae of mayflies were assigned to size classes as they do not have easily distinguishable cohorts (Benke & Jacobi, 1986). The size classes of *Caenis* spp. and the instars of Trichoptera and Lepidoptera were assigned on the basis of head capsule widths (HCW) as they were often reported to be more reliable than body length in separating the different stages (Bradbeer & Savage, 1980; Bass *et al.*, 1982).

Measures of HCWs were made at their widest point including the eyes (Smock, 1980; Bass *et al.*, 1982). All measures were made with an accuracy of 0.025 mm using a dissecting microscope with a micrometer.

Head capsules widths of *Caenis* spp. were divided into 18 classes of 0.05 mm each (Table 1). Larvae of *Mystacides* spp. and *Oecetis* spp. were divided into five larval instars (Table 2). At instar I, genera could not be keyed to species, so they were termed "juveniles".

TABLE 1

Correspondance between size classes and head capsule widhts (HCW) of *Caenis* spp.

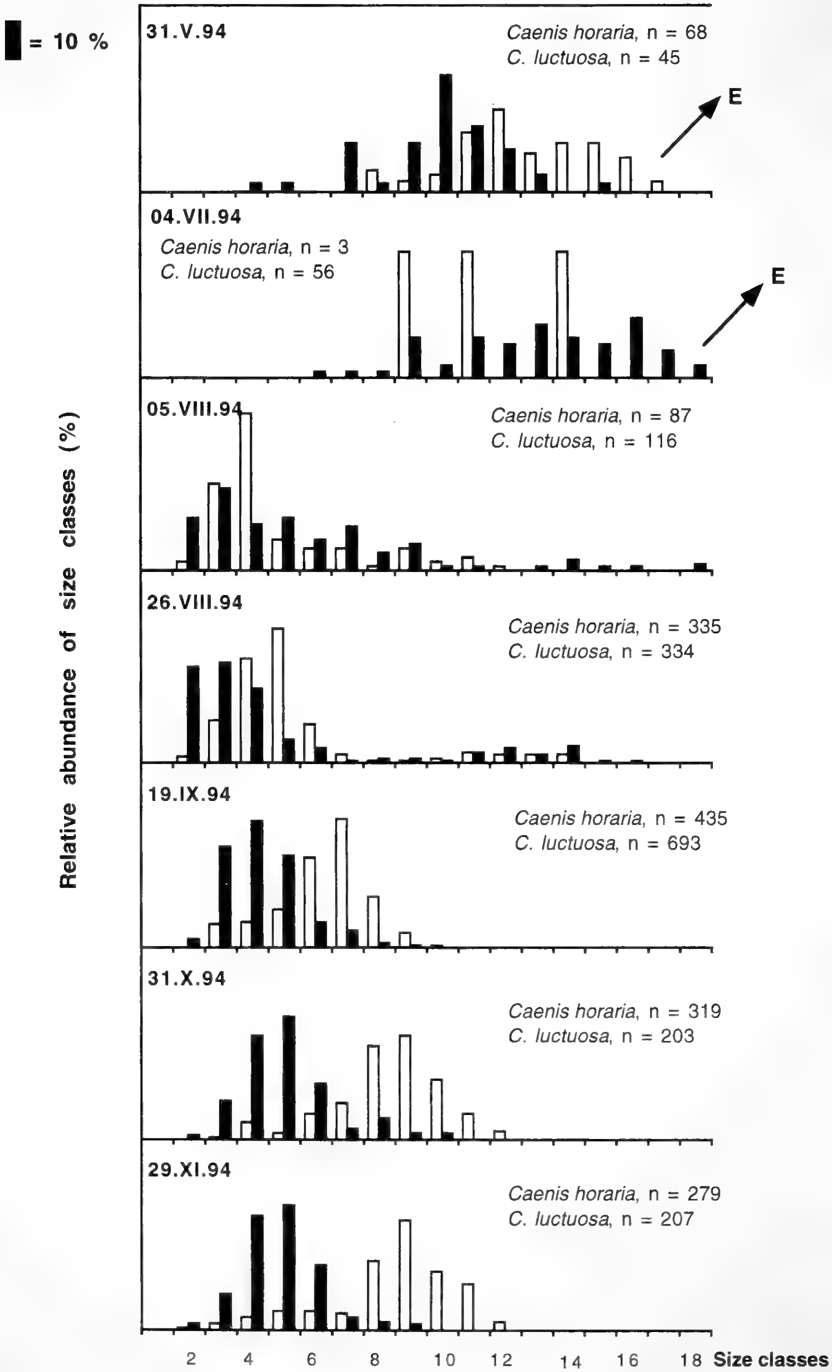
size classes	HCW of *Caenis* spp. (mm)	size classes	HCW of *Caenis* spp. (mm)	size classes	HCW of *Caenis* spp. (mm)
1	0.125 - 0.2	7	0.575 - 0.65	13	1.025 - 1.1
2	0.2 - 0.275	8	0.65 - 0.725	14	1.1 - 1.175
3	0.275 - 0.35	9	0.725 - 0.8	15	1.175 - 1.25
4	0.35 - 0.425	10	0.8 - 0.875	16	1.25 - 1.325
5	0.425 - 0.5	11	0.875 - 0.95	17	1.325 - 1.4
6	0.5 - 0.575	12	0.95 - 1.025	18	1.4 - 1.45

Data in the literature dealing with HCWs of *A. ephemerella* were scarce. Five instars were reported in the literature and Haenni (1974, 1980) identified the sizes of the different instars by collecting individuals in the field and by rearing them.

TABLE 2

Correspondance between instars and head capsule widhts of *Mystacides azurea*, *M. longicornis*, *Oecetis lacustris* and *O. ochracea*.

instars	HCW of *Mystacides azurea* (mm)	instars	HCW of *M. longicornis* (mm)	instars	HCW of *Oecetis lacustris* (mm)	instars	HCW of *O. ochracea* (mm)
juv.	0.125 - 0.175	juv.	0.125 - 0.15	juv.	0.125 - 0.15	juv.	0.125 - 0.2
		II	0.175- 0.2	II	0.175 - 0.2	II	0.25 - 0.3
III	0.2 - 0.275	III	0.25 - 0.325	III	0.25 - 0.35	III	0.375 - 0.475
IV	0.325 - 0.4	IV	0.375 - 0.475	IV	0.4 - 0.525	IV	0.625 - 0.825
V	0.5 - 0.675	V	0.575 - 0.75	V	0.675 - 0.875	V	0.95 - 1.275


= 10 %
Relative abundance of size classes (%)
31.V.94
Caenis horaria, n = 68
C. luctuosa, n = 45
E
04.VII.94
Caenis horaria, n = 3
C. luctuosa, n = 56
E
05.VIII.94
Caenis horaria, n = 87
C. luctuosa, n = 116
26.VIII.94
Caenis horaria, n = 335
C. luctuosa, n = 334
19.IX.94
Caenis horaria, n = 435
C. luctuosa, n = 693
31.X.94
Caenis horaria, n = 319
C. luctuosa, n = 203
29.XI.94
Caenis horaria, n = 279
C. luctuosa, n = 207
2
4
6
8
10
12
14
16
18
Size classes

Combining his results and our measurement yielded the following correspondence between HCWs and instars. Instar I: 0.2-0.3 mm; II: 0.325-0.5 mm; III: 0.525-0.775; IV: 0.8-0.925; V: 0.95-1.1 mm. The different instars are overlapping.

Emergence time of larvae and nymphs was based on numbers and size of the larvae and nymphs at the different sampling sessions.

RESULTS

Comparison of growth and emergence time of congeneric species

The three pairs of congeneric species *Caenis* spp., *Mystacides* spp. and *Oecetis* spp. showed staggering in emergence patterns. This delay was already prepared for in autumn, *C. luctuosa*, *M. longicornis* and *O. lacustris* did stop growing from the middle of September, whereas, *C. horaria*, *M.azurea* and *O. ochracea* showed some growth until October - November.

According to the low numbers catched beginning of July, imagos of *Caenis horaria* emerged between end of May and June. Juveniles appeared in the samples at the beginning of August, but their abundance was highest at the end of August (Fig. 1). At that time, the new generation extended over one month divided into two density peaks: the first one (low density) ranging from size classes 9 to 15 and the second one (high density) ranging from 2 to 8. The nymphs from the first (9-15) peak emerged by the middle of September. Nymphs of the second peak grew until the end of October. Most of them entered the winter period at size classes from 8 to 11.

Caenis luctuosa emerged later than *C. horaria*: at the beginning of July. Juveniles were collected in the samples at the beginning of August, as for *C. horaria*. The two species followed the same growth schedule (with two size class peaks at the end of August) until the middle of September. At that time *C. luctuosa* stopped growing, thus entering the winter period at size classes from 3-8 essentially.

Interpretation of the growth of *Mystacides azurea* was more difficult as sampling in May seemed to have bypassed the emergence of *M. azurea* (Fig. 2). *M. longicornis* emerged at the beginning of July and the first hatched larvae of *M. azurea* were ready to emerge at the beginning of August. Some *M. longicornis* larvae did also reach instar V at the end of August and emerged or disappeared until the middle of September. By the end of October, instars II to IV of *M. longicornis* and III and IV of *M. azurea* were present. *M. longicornis* did not grow further, whereas *M. azurea* was found from instars II to V at the end of November. Entering the winter in the last instar could preclude to an early emergence in spring.

In *Oecetis* spp., emergence time extended from the end of May through August for *O. ochracea*, while the emergence of *O. lacustris* was observed from beginning of July through August. Some of the first hatched larvae of the two species appeared at the

Fig. 1

Size classes and headcapsule widths of *Caenis horaria* (open columns) and *C. luctuosa* (dark columns). Black arrows: emergence.

beginning of August. *O. lacustris* did not grow further from the middle of September and overwintered in the instars II and III, while growth of *O. ochracea* lasted until the end of October and it overwintered in the instars III and IV.

GROWTH AND EMERGENCE OF *ACENTRIA EPHEMERELLA*

End of May was the end of the emergence period for *A. ephemerella* (Fig. 2). There were still some pupae found. At the beginning of July, the first new larvae

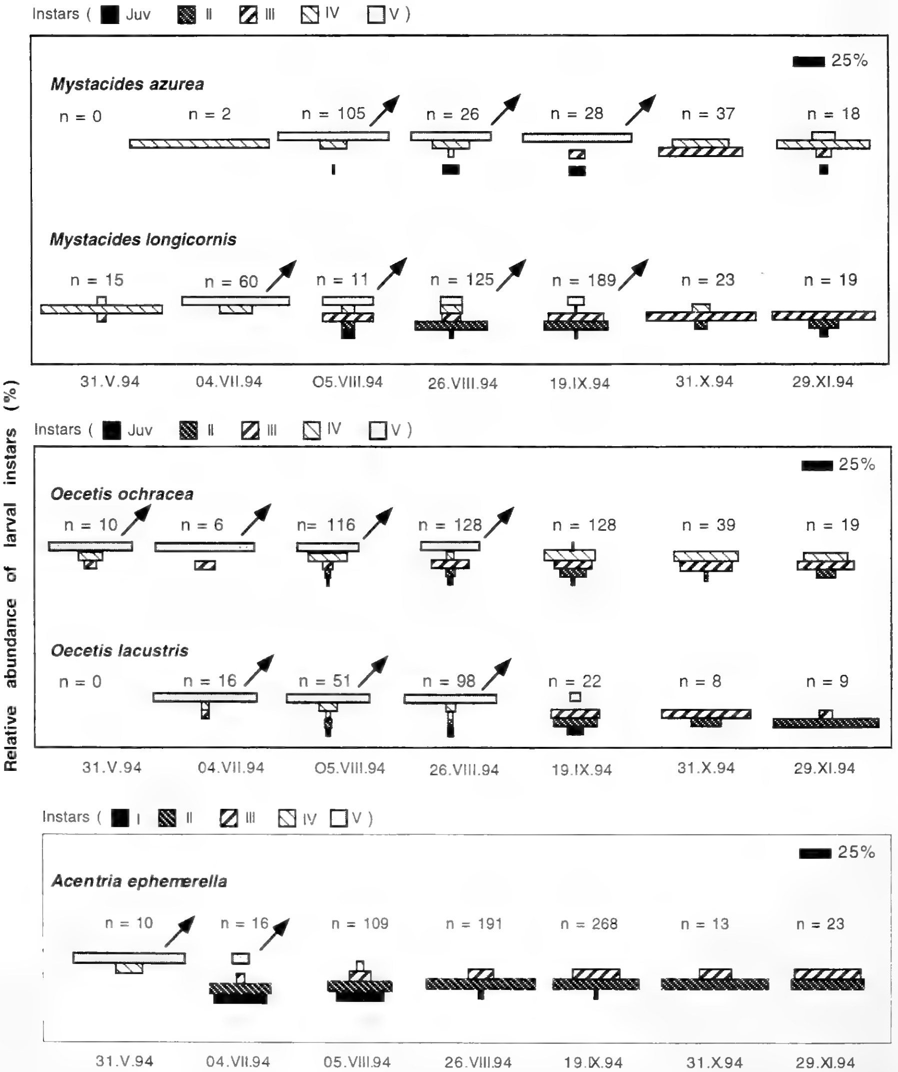


FIG. 2. Frequency of the instars of five insect species (*Mystacides azurea*, *M. longicornis*, *Oecetis lacustris*, *O. ochracea* and *Acentria ephemerella*). Juv.: indetermined juveniles of either *Mystacides* spp. or *Oecetis* spp. Black arrows: emergence.

appeared and at the beginning of August, all larval instars were present. The question remained whether instar V larvae were the first hatched of the 1994 cohort or the last hatched of the 1993 cohort. From August to November, young larvae grew to instar II and III and instar IV larvae disappeared. Abundance of instar II and III larvae was similar at the end of November.

Spatial distribution of instars

None of the seven insect species studied showed significant differences in relative abundance of the different instars or size classes between edge and centre of the macrophyte bed and the adjacent substrate. Our data and figures did however show higher relative abundances of instar V larvae on the plants (edge and centre), especially for *Oecetis* spp. and *Mystacides* spp. (Fig. 4).

Caenis spp. showed no tendency to colonize either plants or adjacent sediments (Fig. 3) and *Acentria ephemerella* was found quite exclusively on the plants (Fig. 5). *M. azurea* was slightly more abundant on the adjacent sediments and on the plants in the edge at the beginning of August, whereas *M. longicornis* was more abundant in the centre at instar V. Thus, it seemed to emerge in higher densities from the centre of the macrophyte bed than *M. azurea.*

Oecetis spp. were the only species which were quite abundant in the sediments. In May, they were mostly emerging from the sediments and in the subsequent sampling periods they were present in higher densities on the macrophytes, mainly at instar V. The bulk of emergence of *O. lacustris* originated from the edge, while *O. ochracea* emerged indifferently from the edge or the centre of the macrophyte bed.

Acentria ephemerella showed highest densities throughout the sampling sessions in the centre of the macrophyte bed, but at the end of May it was mainly found in the edge, besides of the pupae which were found in the centre. Only one individual was found at the beginning of August on the adjacent sediments.

DISCUSSION

The distribution of larval instars and size classes of the investigated congeneric insect species showed that temporal spacing of emergence was a major factor involved in their segregation. Indeed, several authors pointed out the importance of separated swarming in order to optimise mating success (Brittain, 1982). Moreover, the instar segregation already took place in autumn which allows to minimise resource depletion by similarly sized and similarly feeding larvae in winter when food sources are scarce. In *Oecetis* spp., this difference was enhanced by the lower size of *O. lacustris* (usually instar V larvae of *O. lacustris* had the size of instar IV larvae of *O. ochracea*). Size differences between species were lower for the two other congeneric species studied (*Mystacides* spp. and *Caenis* spp.).

The spacing of emergence involved that some species (i.e. *Oecetis* spp.) emerged before macrophyte resumed growth and they therefore did not need the presence of plants to complete their development. However, once the macrophytes were well established, *Oecetis* spp. and *Mystacides* spp. were found on macrophytes prior to

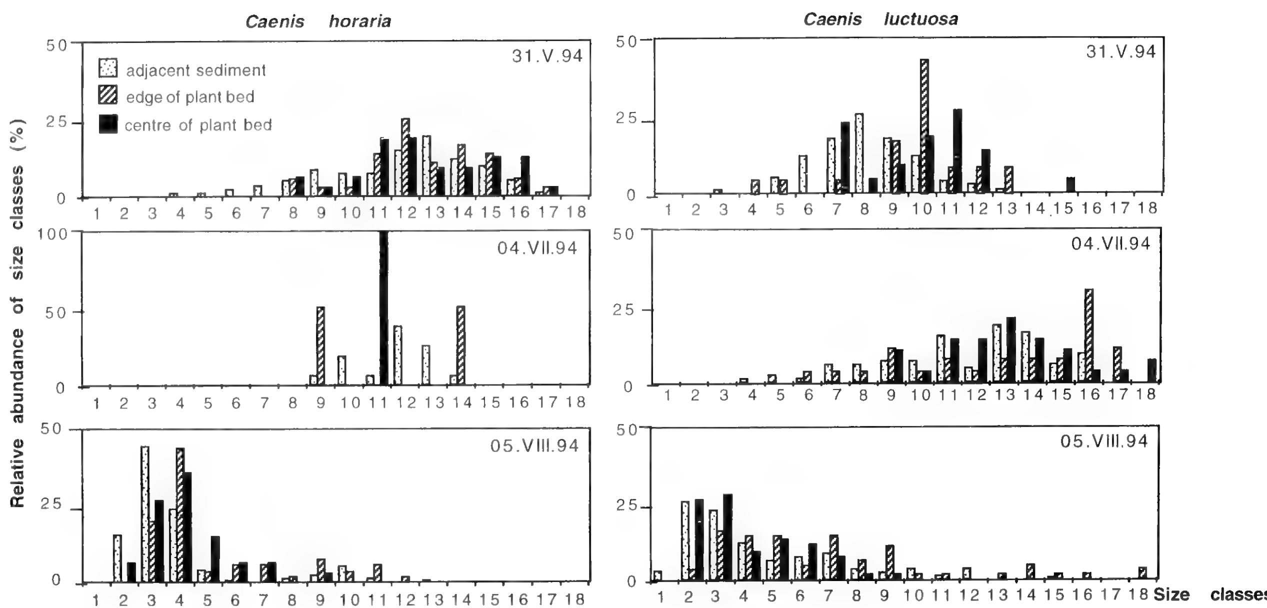


FIG. 3
Frequency of different size classes of *Caenis horaria* and *C. luctuosa* in the edge and in the centre of the macrophyte bed and on the adjacent sediment.

emergence. This may be ought to the advantage of the closer distance to the air-water interface which makes emergence easier and reduces the danger of predation (Rooke, 1984).

Among the seven species studied only two are known to mostly rely on macrophytes for feeding: *Mystacides longicornis* and *Acentria ephemerella*. Thus the main food resource in relation with macrophytes (i.e. plant tissue and periphyton) was not competed for to complete development (Berg, 1941; McGaha, 1952; Lepneva, 1966). The absence of difference in spatial distribution of congeneric taxa may either indicate that there is no spatial segregation or that it occurs at the microhabitat scale, as observed by Hildrew & Edington (1979) in rivers, rather than at the edge and centre scale of macrophyte beds. As Magdych (1979) and Müller-Liebenau (1956) reported, spatial segregation may take place between leaves, stems and roots at different heights (top, middle, bottom) of the plant.

Some instar I larvae of *Oecetis* spp. and *Mystacides* spp. may have been overlooked, thus biasing abundance data on the distribution of juveniles (Bass *et al.*, 1982).

Caenis spp. showed higher densities on the sediments. They emerged from any substrate and except for emergence and hibernation, their size classes were synchronised. The separation of the newly hatched nymphs into a fast growing (emerging after two months) and slow growing (hibernating) generation was already evidenced for *C. horaria* by Oertli (1992) in ponds of the Geneva area. Landa (1968) observed the same pattern for *C. horaria* during its study on central Europe Ephemeroptera. The variable life cycle patterns of Caenidae were reported by many authors (see Clifford, 1982). Thus, it is interesting to note at least identical patterns in different years and biotopes, but in the same area (i.e. Geneva), for one species.

Oecetis spp. illustrated the movement of larvae between the sediments and the macrophytes. Last instar larvae were more abundant on the sediments in May than in the subsequent sampling periods. It is likely that the larvae of *O. ochracea* did not have enough time (or food) to colonize the macrophytes early in the season and therefore they were still found on the adjacent sediments at the time of emergence. *O. lacustris* which emerged at the beginning of July, was able to emerge partly from the macrophytes. *O. ochracea* seemed to be clearly bivoltine, whereas *O. lacustris* showed a mainly univoltine pattern. These two species are at least partly predators so they are not relying on macrophytes for feeding (Mackay & Wiggins, 1970).

M. longicornis, which was found in substantially higher densities on macrophytes than on sediments (Bänziger, 1998), seemed to be synchronised with macrophyte growth. It emerged only once the macrophytes were established, and newly hatched larvae seemed to grow fast enabling them to emerge between the end of August and September. Thus this species showed a fast summer generation and a slower growing winter generation. *M. azurea* was more abundant on adjacent sediments than on macrophytes. It seemed to emerge early and grow slowly, as a limited number of larvae from the year emerged until autumn. Fast growth of *M. longicornis* and slow growth of *M. azurea* were also reported from Petersson (1989) in southern Sweden.

This study showed that closely related taxa with similar ecological niches may coexist in macrophyte beds at some developmental stages. Thus competition seemed

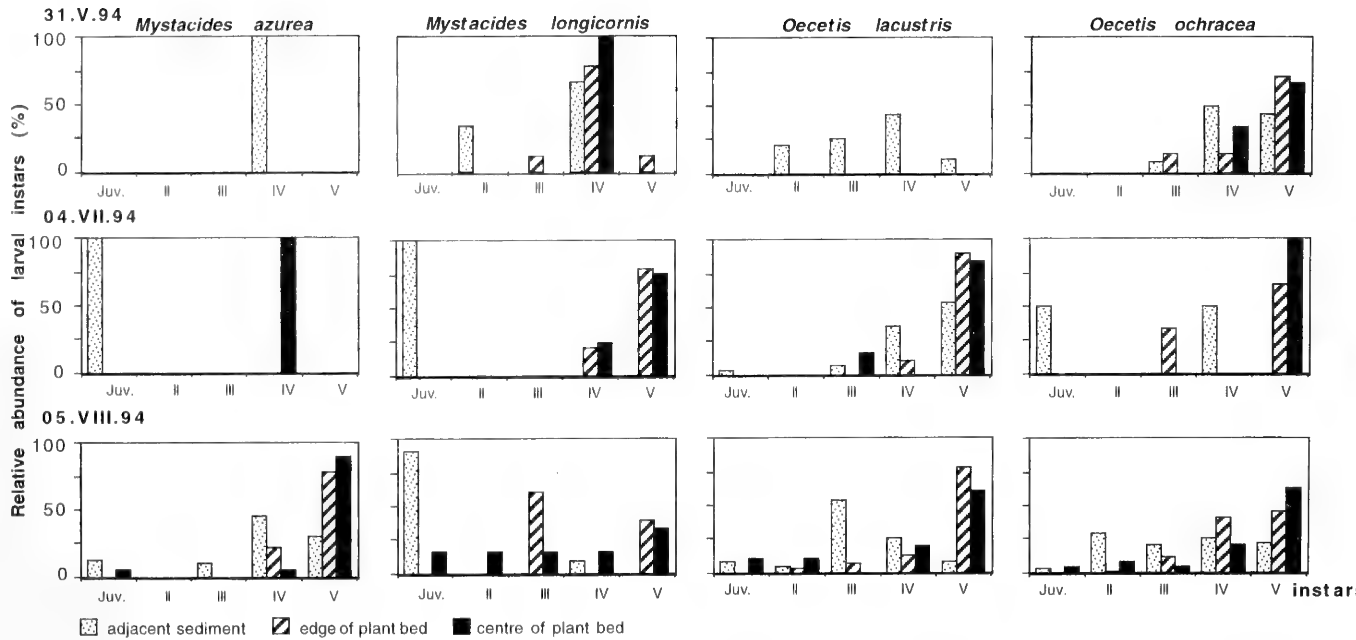


FIG. 4

Frequency of different larval instars of Trichoptera (*Mystacides azurea*, *M. longicornis*, *Oecetis lacustris* and *O. ochracea*) in the edge and in the centre of the macrophyte bed and on the adjacent sediment. Juv.: *Mystacides* spp. or *Oecetis* spp.

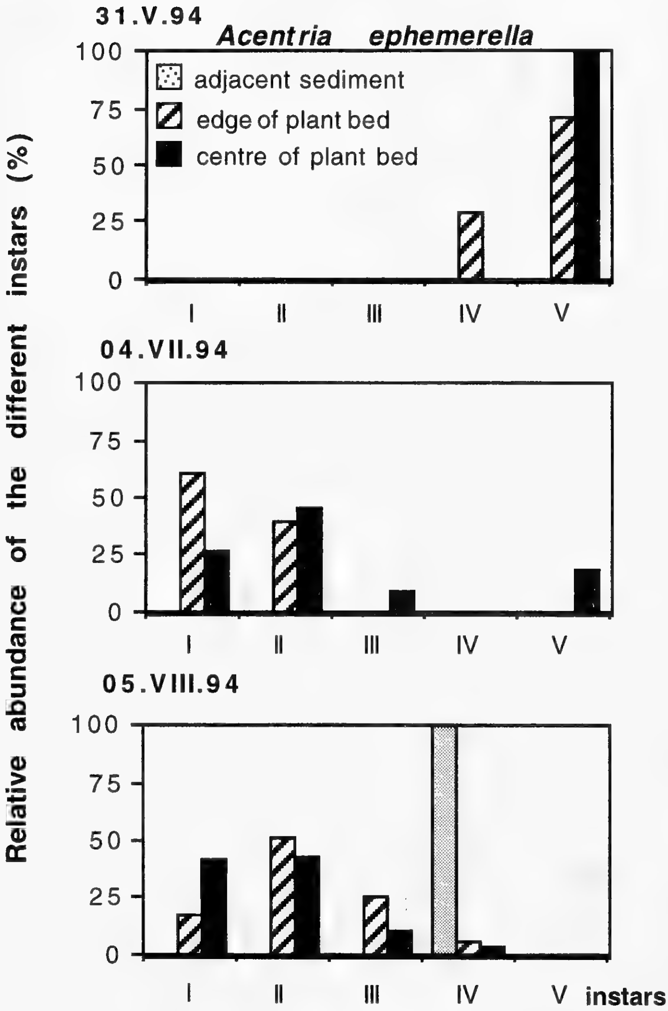


FIG. 5
Frequency of different larval instars of *Acentria ephemerella* in the edge and in the centre of the macrophyte bed and on the adjacent sediment.

not to be involved in species distribution during most of the invertebrate life cycle. Several papers dealing with invertebrate distribution on macrophytes in lakes conclude at an absence of competition in this habitat (Magdych, 1979). Hargeby (1990) explained this absence of competition by the yearly disturbance undergone by the invertebrates through the annual life cycle of the macrophytes. Each year colonization has to be resumed and competition has not enough time to take place (Pickett & White, 1985).

Temporal segregation occurred, however, between congeneric species before hibernation and during emergence. It may allow better resource partitioning when resources are scarce in winter and when maximum energy and food is needed just before emergence. Though there was a tendency for some taxa to live on the edge or on the adjacent sediment at small size classes and to be more abundant in the centre at the last instars or bigger size classes, this (statistically unconfirmed) result may be biased by the impact of predation at the edge on large and moving insects.

ACKNOWLEDGEMENTS

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Les *Nanophthalmus* Motschulsky d'Europe (Coleoptera, Scydmaenidae)

Claude BESUCHET[1] & Stanislav VIT[2]
[1] Muséum d'histoire naturelle, case postale 6434, CH-1211 Genève 6.
[2] Rue de la Poterie 26, CH-1202 Genève.

European species of the genus *Nanopthalmus* Motschulsky (Coleoptera, Scydmaenidae). - Two new species of the genus *Nanophthalmus* Motschulsky, 1851, *N. nonveilleri* sp. n. et *N. serbicus* sp. n. are described from Yugoslavia (Serbia), *N. ditomus* Saulcy, treated previously as synonym of *N. megaloderoides* Motschulsky is revalidated and the lectotype of the species designated. Additional data related to *N. megaloderoides* Motschulsky, *N. turcicus* Reitter and *N. beszedesi* Reitter are provided together with a key to all treated species.

Key words: Coleoptera - Scydmaenidae - Cephenniini - *Nanophthalmus* - taxonomy - Europe.

INTRODUCTION

Seulement sept espèces ont été décrites dans le genre *Nanophthalmus* Motschulsky, 1851: *megaloderoides* Motschulsky, 1851 de Crimée (espèce-type); *ditomus* (Saulcy, 1878) du Caucase; *rotundicollis* (Reitter, 1881) de Talysch; *armeniacus* Reitter, 1884 du Caucase; *turcicus* Reitter, 1894 de Turquie d'Europe; *robustus* Roubal, 1913 du Caucase et *beszedesi* Reitter, 1913 de l'Istrie. Mais plusieurs espèces nouvelles ont été découvertes au cours des vingt dernières années, par le Professeur Guido Nonveiller en Serbie, par M. Rudolf Rous dans le Caucase, par M. Antoine Senglet dans le nord de l'Iran, et enfin par nous en Turquie d'Asie. Des lacunes importantes sont ainsi comblées dans l'aire de répartition du genre *Nanophthalmus*.

Nous avons commencé la révision de ce genre, devenue indispensable. Mais l'échéance du "Catalogue of the Palearctic Coleoptera", nous contraint à une première mise au point, à savoir la redescription des *Nanophthalmus megaloderoides* Motschulsky, *turcicus* Reitter et *beszedesi* Reitter, la revalidation de *N. ditomus* Saulcy et la description de deux espèces nouvelles de Serbie. Ces six *Nanophthalmus* appartiennent au groupe d'espèces de petite taille, ne dépassant en général pas 1 mm.

Manuscrit accepté le 09.02.1999

MATÉRIEL ET MÉTHODES

Abréviations utilisées:

HNHM	Hungarian Natural History Museum, Budapest, Hongrie
IPVB	Institut pour la Protection des Végétaux, Belgrade, Yougoslavie
MHNG	Muséum d'histoire naturelle, Genève, Suisse
MNHN	Muséum National d'Histoire naturelle, Paris, France
MCSN	Museo Civico di Storia Naturale "Giacomo Doria", Gênes, Italie
MSNT	Museo Civico di Storia Naturale, Trieste, Italie
NHMW	Naturhistorisches Museum, Wien, Autriche
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Allemagne
SMFD	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt/Main, Allemagne
ZMHB	Museum für Naturkunde der Humboldt Universität, Berlin, Allemagne

Autres abréviations: A. - antennes; E. - élytres; Lo. - longueur; La. - largeur; P. - pronotum; les étiquettes des matériaux étudiés sont citées ici de manière strictement conforme à l'original:/.../.- étiquette citée; /"...."/ - passages manuscrits de l'étiquette.

DESCRIPTIONS

Genre ***Nanophthalmus*** Motschulsky, 1851 — Figs 1, 2

Nanophthalmus Motschulsky, 1851: 506; espèce-type *Nanophthalmus megaloderoides* Motschulsky, 1851, par monotypie.
Cephennium (Nanophthalmus), Reitter, 1881: 554
Nanophthalmus, Cziki, 1919:17
Nanophthalmus, Lazorko, 1962: 277
Nanophthalmus, Newton & Franz, 1998: 143

Diagnose. Scydmaenidae Cephenniini anophtalmes et aptères. Tête petite, les tempes saillantes. Antennes (Fig. 1) de 11 articles, la massue bien développée, formée de deux articles seulement. Pronotum nettement convexe, un peu moins large que les élytres; côtés arrondis, finement rebordés; aucune ornementation particulière sur le pronotum; pas d'apophyse prosternale. Elytres convexes, sans carène latérale, ornés chacun d'une petite fossette basale profonde, tomenteuse, accompagnée du côté externe d'une carénule très courte; pas de carène humérale à proprement parler mais un pli normalement caché sous la base du pronotum; apex des élytres souvent rebordé. Edéage formé d'une grande capsule basale plus ou moins nettement prolongée par une sorte de manchon dans lequel se trouve l'armure copulatrice; paramères grêles, atteignant l'apex de l'édéage, terminés par une soie.

Nanophthalmus megaloderoides Motschulsky, 1851 — Fig. 3

Nanophthalmus megaloderoides Motschulsky, 1851: 506
Nanophthalmus megaloderoides; Motschulsky, 1869: 271;
Cephennium (Nanophthalmus) megaloderoides; Reitter, 1881: 555;
Cephennium (Nanophthalmus) megaloderoides; Reitter, 1884:84;
Nanophthalmus megaloderoides; Lazorko, 1962: 314-316, fig. 15;

MATÉRIAUX EXAMINÉS: Type perdu. (Loc.typ. Ukraine, Aloupka). 31 ex. /Iaila Gebirge, Krim, Winkler/ (HNHM, MCSN, MHNG, MSNT, NHMW, SMFD, ZMHB).

La collection Victor de Motschulsky du Muséum de Moscou ne renferme aucun exemplaire du genre *Nanophthalmus* et l'exemplaire ayant servi à la description originale semble perdu. L'espèce a été décrite de la Crimée (Tauride, Aloupka). Reitter (1881) n'a pas dû voir des exemplaires de Motschulsky comme le montre sa description qui n' est en fait qu'une mise en commun des données publiées par Motschulsky et de Saulcy (*ditomus*). La diagnose ultérieure et l'édéage publiés pour l'espèce *megaloderoides* Motschulsky par Lazorko (1962) s'appuient sur des exemplaires provenant des Monts Aj Petri, pris par Moczarski et Winkler en mai 1911, qui figurent dans diverses collections, étiquetés collectivement Iaila-Gebirge Krim, Winkler (ou) Moczarski. Ces exemplaires concordent avec la description originale et appartiennent à une seule espèce, bien caractérisée par son édéage, la seule du genre *Nanopththalmus* connue jusqu'à présent de la Crimée. C'est l'espèce la plus occidentale des territoires septentrionaux de la Mer Noire.

DIAGNOSE. Longueur (tête comprise) 0,87-0,97 mm. Elytres moins allongés que chez les espèces balcaniques, ratio E.Lo./E.La. = 1,34-1,41; extrémités apicales des élytres faiblement modifiées, bords épaissis sans être nettement relevés. Pronotum sur la ligne médiane à peu près aussi long que large à la base; côtés du pronotum arqués, convergeant en arrière vers les angles postérieurs; base droite, ratio P.Lo./P.La. = 0,78-0,88; largeur du pronotum subégale ou inférieure à la longueur des antennes; dépressions basales des élytres effacées; angles huméraux avec une fine carène prolongée en arrière.

Antennes; ratio A.Lo./ P.base = 1,14-1,34; articles 3-8 courts, suboblongs ou sphériques, article 9 petit et subsphérique chez les mâles, plus grand, pyriforme et plus transverse chez les femelles; article 11 allongé.

Face ventrale: carénules du métasternum courtes et écartées.

Caractères sexuels des mâles. Protibias recourbés et plus brusquement renflés dans la moitié apicale; face ventrale de la portion basale du profémur pourvue d'une fine carène terminée distalement par une minuscule saillie obtuse; métasternum amplement déprimé (aplati chez la femelle).

Edéage (Fig. 3).

DISTRIBUTION. Ukraine, Crimée méridionale: Iaila Gebirge = Monts Aj Petri (nom actuel). Aloupka = Alupka, la localité typique, se trouve sur le versant sud de cette chaîne monagneuse.

Nanophthalmus ditomus (Saulcy, 1878) Fig. 4

Cephennium ditomum Saulcy, 1878: 139-140, pl. II, fig. 21

Cephennium (Nanophthalmus) megaloderoides Motschulsky = *ditomum* Saulcy; Reitter, 1881: 555

Cephennium ditomum Saulcy = ? *Cephennium (Nanophthalmus) megaloderoides* Motschulsky; Lazorko, 1962: 316

MATÉRIEL ÉTUDIÉ. Lectotype (par présente désignation) ♂: (sans provenance), /disque or/, /"ditomum n. sp. Saulcy, Typ."/,/"14" (étiquette bleue et noire)/, /Typus (étiquette rouge)/, /MUSEUM

DE PARIS 1900 coll. J. CROISSANDEAU/. (MHNP); 1♂, 1♀, /disque or/, /disque bleu/ ,/"Caucase" (étiquette rose)/, /"Cephenn. ditomum Slcy - Cauc (Rtt)"/, /"14" (étiquette bleue et noire)/, /(étiquette rouge vide)/, /MUSEUM DE PARIS 1900 coll. J. CROISSANDEAU/; 1♂, /disque or/, /Caucasus, Meskisches Geb. Leder, (Reitter)/, /"Cephenn. ditomum Saulcy, Caucas"/,/"29" (étiquette bleue et noire)/, /(étiquette bleue)/, /MUSEUM DE PARIS 1900 coll. J. CROISSANDEAU/; 1♂, /disque or/, /Caucasus, Meskisches Geb. Leder, (Reitter)/, /"14" (étiquette bleue et noire)/, /MUSEUM DE PARIS 1900 coll. J. CROISSANDEAU/ (tous les exemplaires MNHN). Autres:8♂♂, 12♀♀, /Caucasus, Meskisches Geb. Leder (Reitter)/, (MNHN, MHNG, NHMW, HNHM, MCSN).

Nanophthalmus ditomus Saulcy est une bonne espèce. Nous avons pu examiner des matériaux de l'époque, retrouvés dans la collection Croissandeau, et constater que la mise en synonymie de cette espèce par Reitter (1881:555) n'était pas fondée. Faute de matériel disponible de Suram, localité-type de *ditomus*, Lazorko (1962:316) maintient formellement la synonymie de Reitter tout en soulignant son caractère douteux. Nous avons choisi pour lectotype un mâle de la collection Croissandeau du Muséum de Paris, portant l'étiquette manuscrite de Saulcy (voir ci-dessous).

DIAGNOSE. Longueur (tête comprise) 0,92-0,99 mm (Saulcy 0.75 mm!). Elytres moins allongés, ratio E.Lo./E.La. = 1,35-1,45; extrémités apicales des élytres modifiées, bords faiblement rebordés et relevés. Pronotum sur la ligne médiane plus court que large à la base; côtés du pronotum arqués, convergeant en arrière vers les angles postérieurs; base droite, ratio P.Lo./P.La. = 0,81-0,86; largeur du pronotum généralement légèrement supérieure ou tout au plus égale à la longueur des antennes; dépressions basales des élytres pratiquement indistinctes; angles huméraux tout au plus avec une très courte carène.

Antennes distinctement plus longues que le pronotum sur la ligne médiane ou sa largeur basale, ratio A.Lo./P.base = 1,05-1,19; articles 3,4 et 5 suboblongs, 6,7 et 8 courts, subsphériques; article 9 généralement assez gros, subpyriforme et transverse chez le deux sexes; article 11 un peu plus long que large.

Face ventrale: carénules du métasternum courtes et écartées.

Caractères sexuels des mâles. Protibias faiblement recourbés, apex avec une protubérance dentiforme; face ventrale de la portion basale du profémur avec une fine carène s'estompant distalement; métasternum amplement concave (faiblement convexe chez la femelle).

Edéage (Fig. 4).

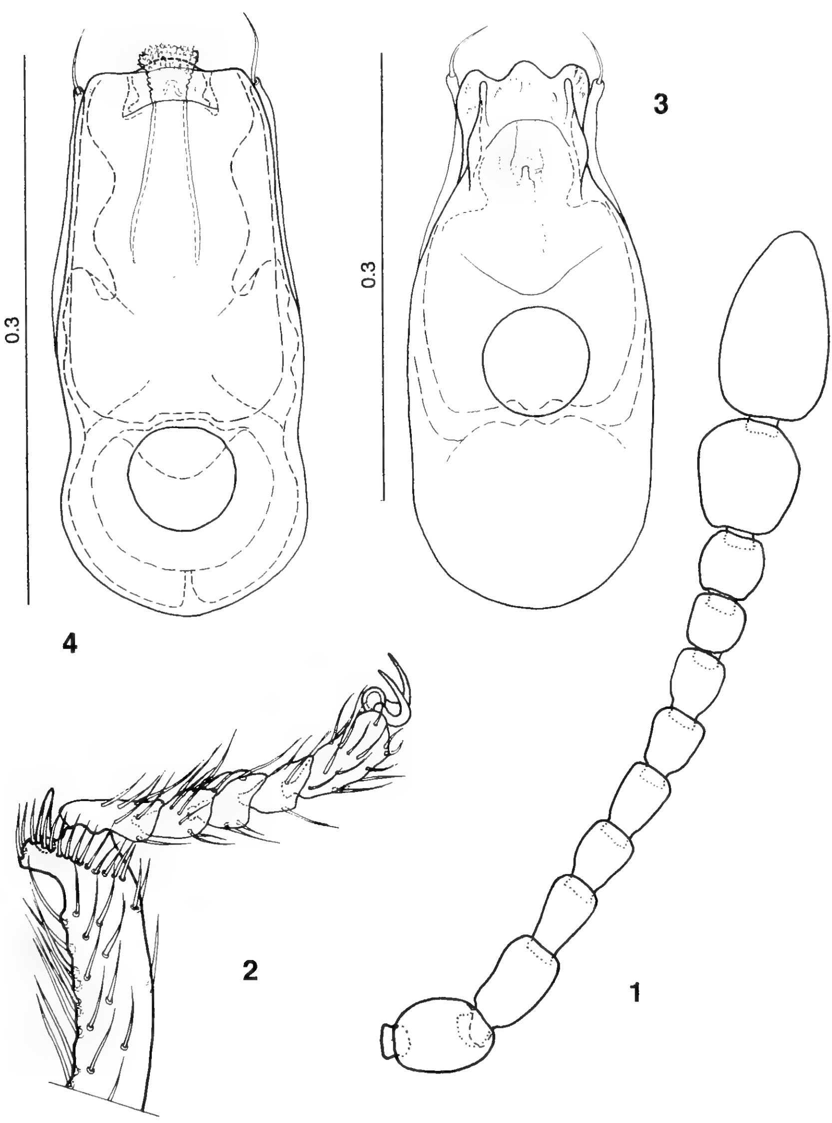
DISTRIBUTION. Géorgie, Suram (localité-type), situé à l'extrême nord-est de Meshedskiy Khrebet (= Meskisches Gebiet des auteurs allemands).

Nanophthalmus turcicus Reitter, 1894 — Fig. 5

Nanophthalmus turcicus Reitter, 1894: 114.

MATÉRIEL ÉTUDIÉ. Holotype ♂ étiquetté:/"Nanophthal. turcicus m. 1894"/, /"Eur. Turkei Merkl."/, /disque or/, /MUSEUM DE PARIS 1900 coll. J. CROISSANDEAU/. (MNHN) /Typus/"turcicus Rtt." Cl. Besuchet dét. XII. 1957/. (MHNP); 2♂♂, 1♀ / "Belgrader Wald près Istanbul, 8.V.58, H. Schweiger"/. (MHNG).

DIAGNOSE. Longueur (tête comprise) 0,94-1,05 mm (Reitter 0,8 mm!). Elytres moins allongés, ratio E.Lo./E.La. = 1,28-1,38; extrémités apicales des élytres à peine



FIGS 1-4

1. *Nanophthalmus* sp., antenne; 2. *Nanophthalmus* sp., apex du protibia; 3. *Nanophthalmus megaloderoides* Motschulsky, édéage face ventrale; 4. *Nanophthalmus ditomus* (Saulcy), édéage face ventrale. (Echelle en mm).

modifiées, simplement renflées. Pronotum sur la ligne médiane aussi long que large à la base; côtés du pronotum arqués, convergeant en arrière vers les angles postérieurs; base droite, ratio P.Lo./P.La. = 07,8-0,82; largeur du pronotum légèrement inférieure à la longueur des antennes; dépressions basales des élytres pratiquement indistinctes; angles huméraux tout au plus avec une très courte carène.

Antennes très nettement plus longues que le pronotum sur la ligne médiane , ratio A.Lo./P. base = 1,13-1,28; articles 3 et 4 subégaux, oblongs, 7 et 8 courts, subsphériques; article 9 plus gros, transverse chez le deux sexes; article 11 moins d'une fois et demie plus long que large.

Face ventrale: carénules du métasternum courtes mais peu écartées.

Caractères sexuels des mâles: protibias faiblement recourbés et renflés dans leur moitié apicale; crochet apico-interne petit, peu distinct; face ventrale de la portion basale du profémur pourvue d'une fine carène terminée distalement par une minuscule saillie obtuse; métasternum amplement concave chez le mâle, simplement applati chez la femelle.

Edéage (Fig. 5).

DISTRIBUTION. Turquie, Thrace, Forêt de Belgrade près d'Istanbul.

Nanophthalmus beszedesi Reitter, 1913 Fig. 6

Nanophthalmus beszedesi Reitter, 1913: 140-141.

MATÉRIAUX EXAMINÉS. Lectotype (par présente désignation) ♀: étiqueté, /Dr. v. Beszédes, M. Maggiore, Istrien, "15/8"/ Mus. HMHN det. Reitter Nanophthalmus beszedesi. Paralectotype (par présente désignation) 1♀, /idem/, (les deux HNHM). Il s'agit bien des matériaux vus par Reitter qui cite "2 ex. am 15 August v. J.". Autres: 1♂, /Dr. Beszedes, M. Maggiore, Istria "22.V. 1913"/, /"Nanophthalmus Beszedesi Reitter"/. (MHNG); 1♂, /idem/. (MCSN.- coll Dodero); 1♂, /Mte Maggiore, Istr. Winkler. (ZMHB); 3 ex. /Mte Maggiore, Winkler/. (SMFD).

DIAGNOSE. Longueur (tête comprise) 0,87-0,92 mm. Elytres très allongés, ratio E.Lo./ E.La. = 1,48-1,53; extrémités apicales des élytres très nettement modifiées, présentant un fort bourrelet retroussé vers le haut, échancré à la suture. Pronotum sur la ligne médiane aussi long que large à la base; côtés du pronotum fortement arqués au tiers antérieur, subparallèle en arrière avant les angles postérieurs; ratio P.Lo./P.La. = 0,87-0,88; largeur du pronotum égale ou inférieure à la longueur des antennes; callosités humérales distinctes; dépressions basales indistinctes.

Antennes nettement plus longues que le pronotum sur la ligne médiane ou comme sa largeur à la base, ratio A.L/ P.base = 1,14-1,2 ; articles 3, 4 et 5 à peine oblongs, 6, 7 et 8 subsphériques, article 9 petit, subsphérique chez le mâle, plus grand et pyriforme chez la femelle; article 11 court, tout au plus d'un quart plus long que large. Face ventrale: carénules mésosternales prolongeant la lame sternale à peine développées.

Caractères sexuels des mâles. Protibias recourbés, brusquement renflés dès le milieu, apex avec une protubérance dentiforme; face ventrale de la portion basale du profémur sans caractères particuliers; métasternum amplement déprimé (aplati chez la femelle).

Edéage (Fig. 6).

DISTRIBUTION. Croatie, Istrie, Monte Učka, (= Monte Maggiore).

Nanophthalmus nonveilleri sp. n. Figs 7, 8, 11

MATÉRIAUX EXAMINÉS. Holotype. ♂, étiqueté: /Serb. Tara pl., 1000 m, "11.06. 84", Nonvll./ (IPVB); Paratypes. 1♂, 2♀♀, / idem "11.06.84"/. (MHNG); 2♂♂, 2♀♀,./ idem, "23.05. 84"/ (IPVB, MHNG); 1♂, / idem, "6.10. 78"/ (IPVB); 1♂, /Serb. Tara pl., 900 m, "6.10. 78/ (IPVB). 1♂ /Serb. Tara pl., 900 m, "6.10.78/ (IPVB). 1♂, 2♀♀, /Yougoslavie, Serbie: Tara Planina, Mitrovac (route Mitrovac-lac d'accumulation), 900 m, 23.V.1984; tamisage de feuilles mortes dans une forêt de hêtres, érables et épicéas (Besuchet)/. (MHNG).

DIAGNOSE. Longueur (tête comprise) 0,89-1,02 mm. Elytres très allongés, ratio Long./ Larg. = 1,43-1,55; extrémités apicales des élytres non modifiées, simples. Pronotum sur la ligne médiane plus long que large à la base; côtés du pronotum fortement arqués au milieu, convergeant en arrière nettement vers les angles postérieurs; base droite; ratio P.Long./P.Larg. = 0,86-0,91; largeur du pronotum supérieure à la longueur des antennes; base des élytres sans trace de dépression basale ou de callosité humérale.

Antennes un peu ou nettement plus longues que le pronotum sur la ligne médiane et très nettement plus longues que la largeur basale de celui-ci, ratio A.L/ P.base = 1,09-1,34; articles 3, 4 et 5 oblongs, 6, 7 et 8 subsphériques, article 9 transverse, pyriforme, plus nettement transverse semble-t-il chez les mâles et plus allongé chez les femelles; article 11 court, un peu plus long que large.

Face ventrale: carénules du métasternum faiblement divergentes.

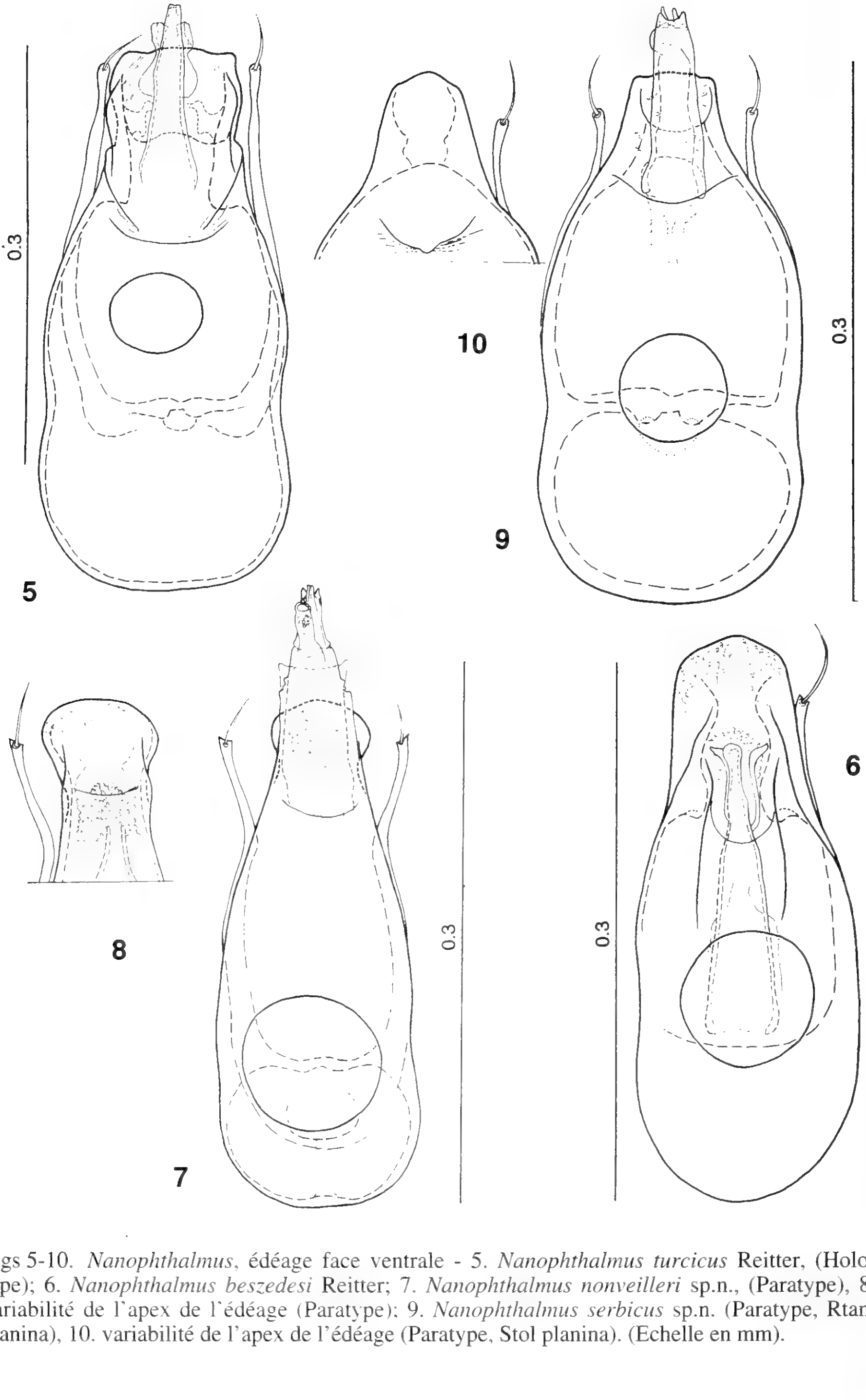
Caractères sexuels des mâles. Protibias recourbés, nettement renflés dans la moitié distale, pourvus de crochet apical; face ventrale de la portion basale du profémur avec une fine carène s'estompant distalement; métasternum peu différencié, à peine aplani chez le mâle (faiblement convexe chez la femelle).
Edéage. (Figs. 7, 8).

DISTRIBUTION (Fig. 11). Serbie occidentale:Tara planina ((8) localité-type). Selon Dr. G. Nonveiller (communication personnelle) cette espèce se rencontre aussi à Goc planina, Beli izvori et Dobre vode (9); Ivanjica, Mucina voda (10); Ovcar Banja, Ovcarsko-Kablarska klisura, Debela Gora (11). Elle va de 600 à 1000 m d'altitude. (Ces exemplaires ont été capturés et determinés par MM. Nonveiller et Pavicevic et sont déposés à IPVB).

Nanophthalmus serbicus sp. n. Figs 9, 10, 11

MATÉRIAUX EXAMINÉS. Holotype: ♂, étiqueté /Serb. Stol pl., 800 m, Nonvll., "26.05. 1984"/. (IPVB). Paratypes: 1♂, /idem "26.05.1984"/. (MHNG); 2 ex. /idem "10.04.1982"/ (IPVB, MNHG); 3♂♂, 2♀♀, /idem "15.5.1982"/ (IPVB, MHNG); 1♂ /Serb. Rtanj pl. "12.III. 1977."/ (MHNG); 9♂♂, 7♀♀, / Yougoslavie, Serbie: Stol Planina (30 km au nord de Bor), 900 m, 26.V. 1984; tamisage de feuilles mortes au pied de rochers, dans une forêt de hêtres, (Besuchet). (MHNG); 1♂, 3♀♀, / même provenance, 27.V.1984; lavage de terre au pied de vieilles souches de hêtres (Besuchet). (MHNG); 2♂♂, 1♀, /Yougoslavie, Serbie: Rtanj Planina, 600 m, 27.V. 1984; tamisage de feuilles mortes au fond d'un ravin, dans la forêt de hêtres (Besuchet). (MHNG).

DIAGNOSE. Longueur (tête comprise) 0, 92-0,99 mm. Eytres nettement allongés, ratio Long./Larg. = 1,39-1,5; extrémités apicales des élytres à peine modifiées, bords épaissis sans être nettement relevés. Pronotum sur la ligne médiane plus court ou tout au plus aussi long que large à la base; côtés du pronotum fortement arqués dans le tiers anté-



Figs 5-10. *Nanophthalmus*, édéage face ventrale - 5. *Nanophthalmus turcicus* Reitter, (Holotype); 6. *Nanophthalmus beszedesi* Reitter; 7. *Nanophthalmus nonveilleri* sp.n., (Paratype), 8. variabilité de l'apex de l'édéage (Paratype); 9. *Nanophthalmus serbicus* sp.n. (Paratype, Rtanj planina), 10. variabilité de l'apex de l'édéage (Paratype, Stol planina). (Echelle en mm).

FIG. 11

Carte de distribution - espèces de la Serbie: *Nanophthalmus serbicus* sp. n. (No. 1 - 7); *Nanophthalmus nonveilleri* sp. n. (No. 8 - 11).

rieur, presque subparallèles avant les angles apicaux, base droite, ratio P.Long./ P.Larg. = 0.81-0,86; largeur du pronotum subégale ou légèrement inférieure à la longueur des antennes; angles huméraux oblitérés, nuls; dépressions basales des élytres faibles.

Antennes très nettement plus longues que le pronotum sur la ligne médiane et nettement plus longues que sa largeur basale, ratio A.L/ P.base = 1,08-1,33; articles 3, 4 et 5 oblongs, 6, 7 et 8 subsphériques, article 9 petit, subsphérique à faiblement transverse chez les mâles, plus grand, pyriforme et plus nettement transverse chez les femelles, article 11 court, pratiquement aussi large que long.

Face ventrale: carénules du métasternum fortement divergentes.

Caractères sexuels des mâles. Protibias plus nettement recourbés dans leur portion apicale seulement, nettement renflés dès le milieu, dépourvus d'un crochet apical; face ventrale de la portion basale du profémur avec une fine carène s'estompant distalement; métasternum fortement déprimé, concave (applati chez la femelle,).
Edéage (Figs. 9, 10).

Distribution (Fig 11). Serbie orientale:(1)Stol planina, (localité-type) et (2)Rtanj planina;. Selon Dr. G. Nonveiller (communication personnelle) cette espèce se rencontre aussi à Zajecar- Lenovac (3); Homolje - Ceremosnja (4); Mts. Homolje - Mejdan Kucana (5); Jastrebac planina - Ravniste (6) et Kragujevac - Zezelj (7). Elle va de 450 à 1200 m d'altitude. Ces exemplaires ont été capturés et determinés par MM. Nonveiller et Pavicevic (déposés à IPVB).

TABLEAU DES ESPÈCES CITÉES

Ce tableau n'a qu'une valeur indicative; les identifications doivent être contrôlées par l'édéage.

1 Apex des élytres orné d'un bourrelet fortement développé, relevé vers le haut; Istrie . . . . *beszedesi* Reitter
- Apex des élytres non relevé, tout au plus avec un bourrelet léger 2
2 Elytres plus larges (0,46-0,49 mm), très convexes; Thrace . . . . . *turcicus* Reitter
- Elytres moins larges (0,40-0,43 mm), moins convexes 3
3 Pubescence du pronotum et des élytres formée de soies couchées de longueur moyenne; élytres plus courts (indice élytral 1,35-1,41) 4
- Pubescence du pronotum et des élytres formée de soies semi-dressées assez longues; élytres plus allongés (indice élytral 1,42-1,55) 5
4 Corps moins déprimé (haut. ~ 0,35 mm); en vue latérale la convexité du pronotum est nettement séparée de celle des élytres; Géorgie . *ditomus* (Saulcy)
- Corps relativement déprimé (haut. ~ 0,30 mm); en vue latérale la convexité du pronotum se prolonge sur celle des élytres; Crimée . . . . *megaloderoides* Motschulsky
5 Antennes légèrement plus longues, les articles 6 et 7 légèrement plus longs que larges; métasternum du mâle avec une dépression arrondie profonde; Serbie . . . . *serbicus* sp. n.
- Antennes légèrement plus courtes, les articles 6 et 7 à peine ou légèrement plus larges que longs; métasternum du mâle avec une dépression triangulaire très superficielle; Serbie . . . . *nonveilleri* sp.n.

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Nous tenons à remercier ici toutes les institutions citées, pour nous avoir facilité l'étude des matériaux des collections historiques, traités dans cette note, puis plus particulièrement le Professeur Guido Nonveiller de Zemun et l'Institut pour la Protection des Végétaux de Belgrade, Yougoslavie, pour nous avoir confié l'étude des matériaux provenant de leurs recherches.

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REVUE SUISSE DE ZOOLOGIE 107 (1): 165-211; mars 2000

Über die Lauterzeugung der Welse (Siluroidei, Ostariophysi, Teleostei) und ihren Zusammenhang mit der Phylogenie und der Schreckreaktion *

Andreas HEYD & Wolfgang PFEIFFER
Zoologisches Institut, Universität Tübingen,
Auf der Morgenstelle 28,
D-72076 Tübingen, Germany.

Sound production in catfish (Siluroidei, Ostariophysi, Teleostei) and its relationship to phylogeny and fright reaction. - Sound production by pectoral stridulation, and sound production by swim-bladder mechanisms were studied in 19 species of catfish from 8 families. Stridulation sounds were recorded in air by means of a microphone and a tape recorder while holding one of the pectoral spines; swim-bladder sounds were recorded under water. All sounds were investigated by sonographic analysis of the records. In addition, three species (*Arius seemani*, *Pimelodella gracilis*, *Pimelodus pictus*) were studied anatomically in order to determine whether or not they have a swim-bladder mechanism.

Sound production by stridulation was observed when the enlarged pectoral fin spines were moved in both directions (spread and attracted) in *Mystus gulio*, *M. vittatus* (Bagridae), *Synodontis ocellifer*, *S. schoutedeni* (Mochokidae), *Agamyxis flavopictus* (Doradidae), and *Dysichthys coracoideus* (Aspredinidae). In contrast, the following species produced sounds only when they spread their pectorals: *Arius seemani* (Ariidae), *Pimelodella (= Brachyrhamdia) meesi* (Pimelodidae), *Dianema urostriata* (Callichthyidae), *Peckoltia pulcher*, and *Glyptoperichthys gibbiceps* (Loricariidae). In the other Loricariidae studied sound production was absent.

In addition to the pectoral stridulation mechanism, *Arius seemani* possesses a modified swim-bladder mechanism, called the "Springfederapparat" (Müller, 1842) or „elastic spring apparatus". Thin elastic bones, derived from the transverse processes of the first few vertebrae, function in sound production. Specialized sonic muscles on the upper surface of this „elastic spring" cause the vibration of the swim-bladder. The elastic bones function as antagonists of the muscular contraction. They return the fibres of the sonic muscles after each contraction. The sonic activity of *A. seemani* with its swim-bladder mechanism showed a daily rhythm. The choruses were most vigorous in the early morning. The sounds emitted consisted of short

* In memoriam Prof. Dr. Karl von Frisch

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pulses at irregular intervals with a fundamental frequency near 170 ± 30 Hz. This frequency was equivalent to the vibration frequency of the sonic muscles.

In *Pimelodus pictus* (Pimelodidae) the protractor muscle (functioning as a vibration generator) is directly connected to the swim-bladder (serving as a resonance body). This system generates drumming sounds. In *Pimelodella gracilis* a swim-bladder mechanism could not be found.

We detected a new method of sound production in *Hemibagrus nemurus* (Bagridae). It is able to squeak or to scream by pressing out air from its gill slits.

The frequent occurence of a stridulatory mechanism by means of the pectoral spines in at least 13 out of 33 families of catfish indicates that those species which lack a stridulatory mechanism may have subsequently lost it during evolution. In contrast, swim-bladder mechanisms are supposed to have developed independently several times, since they are differently structured. The existence of two very different sonic mechanisms, a stridulatory as well as a swim-bladder mechanism, in the same species (for example *Arius seemani* and *Pimelodus pictus*) indicates that the sounds may have a different biological significance. The frequencies of the nonharmonic sounds by stridulation (described as chirps, clicks, croaks, grunts, knocks, scrapes, scratches, squeaks, rasps, thumps and so on) range from 100 - 8000 Hz, mostly 1000 - 4000 Hz. Their main acoustic energy is found at frequencies above the hearing range of most fish, except the Ostariophysi. In addition, all predaceous fishing mammals and birds are able to hear these frequencies. Thus, these sounds may serve as an important means of warning and defence, especially since they are mostly produced when the catfish is captured and pulled out of the water. The noise may function in the same way as that produced by threatened rattle snakes. In a similar manner to these poisonous snakes, the stridulating catfish are defensive. The pectoral spines and the dorsal spine are erected simultaneously in order to protect the fish. Since pectoral and dorsal spines have locking mechanisms, predators can swallow these catfish only with great difficulty. Whereas stridulatory mechanisms exist in many solitary species, swim-bladder mechanisms are numerous in social catfish and are supposed to serve intraspecific communication.

In all species of the mostly solitary and night active catfish that have been studied with respect to their sound production, the fright reaction elicited by the alarm substance from the epidermis of conspecifics is either little developed (Mochokidae, Pimelodidae) or absent (Aspredinidae, Loricariidae). On the other hand, no stridulatory mechanism has been detected in some pelagic, schooling species of catfish possessing a distinct, well-developed fright reaction and being active in daylight (*Eutropiellus vandeweyeri* - Schilbeidae, *Kryptopterus bicirrhis* - Siluridae). However, since only a few species of catfish have been studied, conclusions concerning a connection between the existence of the chemically elicited fright reaction

on the one hand and sound production by sonic mechanisms on the other should only be drawn with caution.

Key-words: fish - catfish - sound production - stridulation - swim-bladder mechanisms (Trommelmechanismen) - „elastic spring apparatus" (Springfederapparat) - fright reaction (Schreckreaktion) - alarm substance (Schreckstoff).

EINLEITUNG

Die Welse (Siluroidei) umfassen mit etwa 2500 rezenten Species in 33 Familien (Teugels, 1996) mehr als ein Drittel aller Ostariophysen (Sagemehl, 1885) und ungefähr 10% der Teleostei (Eigenmann & Eigenmann, 1890; Regan, 1911; Berg, 1958; Greenwood *et al.*, 1966; Roberts, 1973; Gosline, 1975; Novacek & Marshall, 1976; Briggs, 1979; Fink & Fink, 1981, 1996; Lauder & Liem, 1983; Lundberg & McDade, 1986; Nelson, 1994). Mehr als 90% der Welsarten sind solitäre, in Bodennähe lebende, nachtaktive, räuberische Süßwasserfische. Viele Callichthyidae, Pangasiidae, Schilbeidae und manche Siluridae sind tagaktiv, schwarmbildend und Kleintier- oder Pflanzenfresser. Die Loricariidae ernähren sich vorwiegend von Pflanzen und Detritus. Einige Ariidae, Aspredinidae und Plotosidae leben im Meer oder Brackwasser (Franke, 1985). Die Plotosidae zeigen im Juvenilstadium ein besonders stark ausgeprägtes Schwarmverhalten (Burgess, 1989). Als Ostariophysi *sensu stricto* (Otophysi *sensu* Rosen & Greenwood, 1970) haben alle Welse einen Weberschen Apparat (Weber, 1820; Wright, 1884; Bridge & Haddon, 1889, 1893, 1894; Sörensen, 1895; Chranilov, 1929; Alexander, 1964, 1965; Chardon, 1968). Er verbindet die Schwimmblase mit dem Innenohr und dient der Steigerung der Hörschärfe (von Frisch & Stetter, 1932). In vielen Welsfamilien gibt es Species, die in ihrer Epidermis Schreckstoffzellen führen (Pfeiffer, 1960, 1970, 1977). Beim Schreckstoff (von Frisch, 1938), der diesen Zellen entstammt (Pfeiffer, 1960; Smith, 1973), handelt es sich um ein Pheromon (Karlson & Lüscher, 1959), das bei Freisetzung durch Hautverletzung eine gesteigerte Aufmerksamkeit und eine Fluchtreaktion der Artgenossen auslöst. Dieses Verhalten wurde von Karl von Frisch (1938, 1941a, b) an der Elritze (*Phoxinus phoxinus*, Cyprinidae) entdeckt und als Schreckreaktion bezeichnet. Während die Schreckreaktion ein Merkmal aller Ostariophysi *sensu lato*, d.h. Gonorynchiformes (= Anotophysi, Rosen & Greenwood, 1970) plus Otophysi, ist (Pfeiffer, 1967), tritt der Webersche Apparat nur bei den Otophysi auf und ist somit das phylogenetisch jüngere Merkmal. Bei einigen Species oder Familien mit besonderer Lebensweise wurde die Fähigkeit zur Schreckreaktion sekundär teilweise oder vollständig rückgebildet (Pfeiffer, 1963a). So fehlt den Serrasalminae und Mylinae nur die Fähigkeit zur Schreckreaktion (im ZNS), obwohl sie in ihrer Epidermis Schreckstoffzellen (histologisch sichtbar) und damit Schreckstoff (im Verhaltensexperiment nachgewiesen) führen (Pfeiffer, 1962a, 1963a; Markl, 1968). Die Gymnotoidei und die Welsfamilien Aspredinidae und Loricariidae haben dagegen im Laufe ihrer Stammesgeschichte auch die Schreckstoffzellen und damit den Schreckstoff rückgebildet (Pfeiffer 1963a). Wie die meisten Knochenfische (Tele-

ostei) besitzen fast alle Welse (mit Ausnahme der Aspredinidae) Mauthner-Axone in ihrem ZNS und damit eine Mauthner-Reaktion, mit der auch ihre Schreckreaktion beginnt (Pfeiffer *et al.*, 1986; Göhner & Pfeiffer, 1996).

Etwas Besonderes innerhalb der Ostariophysi ist die Fähigkeit zahlreicher Welsarten, auf unterschiedliche Weise Laute zu erzeugen. Bei mindestens 8 Familien kommen Trommelmechanismen vor, und noch häufiger treten Stridulationsapparate auf. Innerhalb mehrerer Familien gibt es sogar beide Mechanismen nebeneinander. Ein Trommelmuskelapparat oder Springfederapparat ist bekannt von den Ariidae, Auchenipteridae, Bagridae, Doradidae, Malapteruridae, Mochokidae, Pangasiidae und Pimelodidae (Müller, 1842, 1857; Sörensen, 1884, 1895; Tavolga, 1962; Abu-Gideiri & Nasr, 1973; Kastberger, 1977, 1978; Kratochvil *et al.*, 1980; Schachner & Schaller, 1982; Ladich & Fine, 1994). Die Schwimmblase verstärkt als Resonanzraum die Vibration der mit ihr direkt oder indirekt verbundenen Trommelmuskeln.

Bei der Stridulation werden durch Gegeneinanderreiben von Knochenelementen knarrende Geräusche erzeugt. Am weitesten verbreitet ist die Stridulation mit den Brustflossen. Sie ist nachgewiesen für die Ariidae, Aspredinidae, Auchenipteridae, Bagridae, Callichthyidae, Doradidae, Heteropneustidae, Ictaluridae, Loricariidae, Mochokidae, Pangasiidae und Pimelodidae. Die Laute entstehen durch Bewegung des massiven Kopfes des ersten Brustflossenstrahls (Stachel), der einen Knochenkamm mit Querrillen und Höckern trägt und in eine gebogene Kerbe (Gelenkpfanne) im Cleithrum (Teil des Schultergürtels) eingepaßt ist. Wird dieser Knochenkamm gegen den Boden der Gelenkpfanne gepreßt und gleichzeitig bewegt, entstehen knarrende Geräusche (Geoffroy Saint-Hilaire, 1829; Dufossé, 1874; Haddon, 1881; Sörensen, 1884; Villwock, 1960; Winn, 1964; Pfeiffer & Eisenberg, 1965; Agrawal & Sharma, 1965; Gainer, 1967; Abu-Gideiri & Nasr, 1973; Brousseau, 1976; Kastberger, 1977, 1978; Kratochvil *et al.*, 1980; Kratochvil & Völlenkle, 1981; Schachner & Schaller, 1982; Fine *et al.*, 1996, 1997; Kaatz, 1999). Als Besonderheit ist von einigen Sisoridae die dorsale Stridulation (wie von Geoffroy Saint-Hilaire, 1829 an *Synodontis schall* irrtümlich vermutet) bekannt. Hierbei reibt eine feilenförmige Struktur an der Rückenflossenbasis durch Vor- und Rückwärtsbewegung gegen die gerippte Oberfläche der verwachsenen Neuratfortsätze des Wirbelkomplexes (Haddon, 1881; Mahajan, 1963; Alexander, 1965).

Bei allen Fischen mit besonderen lauterzeugenden Organen handelt es sich um Knochenfische (Osteichthyes), meist Teleostei. Bereits Aristoteles erwähnt sechs lauterzeugende Fischarten (Aristoteles, auch zitiert bei Cuvier & Valenciennes, 1840, Müller, 1857 und Sörensen, 1884, 1895). Es handelt es sich dabei um Species aus dem Mittelmeer. Geoffroy Saint-Hilaire (1829) beschrieb als erster die Lauterzeugung durch Stridulation eines Welses, nämlich *Synodontis schall* (Bloch & Schneider, 1801) aus dem Nil (Daget *et al.*, 1986). Seine richtige Aussage wurde von Cuvier & Valenciennes (1840) ohne eigene Beobachtung abgestritten, doch von Johannes Müller (1857) bestätigt. Erst knapp 100 Jahre nach Geoffroy Saint- Hilaire (1829) hat Karl von Frisch (1923) mit der von ihm in die Sinnesphysiologie und Verhaltensforschung eingeführten genialen Dressurmethode das Hörvermögen für Fische nachgewiesen, und zwar am nordamerikanischen Zwergwels *Ameiurus nebulosus*, "der

kommt, wenn man ihm pfeift" (wofür der geblendete Fisch mit Futter belohnt wurde). Im Gegensatz zu den experimentellen Untersuchungen über Hörvermögen und Lauterzeugung gehen die ersten anatomischen Befunde und Beobachtungen an den lauterzeugenden Organen von Welsen weit mehr als 100 Jahre zurück (Müller, 1842; Agassiz, 1852; Reissner, 1859; Dufossé, 1874; Haddon, 1881; Wright, 1884; Sörensen, 1884, 1895, 1898; Bridge & Haddon, 1889, 1893, 1894).

Eine Tierart bedarf, um zu überleben, des Schutzes ihrer Individuen vor dem Gefressenwerden durch Beutegreifer. Ein Schutz vor räuberischen Überfällen kann gegeben sein durch die Warnung der Artgenossen, beispielsweise durch ein Alarmpheromon wie den Schreckstoff, und ist besonders bei wehrlosen, tagaktiven und schwarmbildenden Fischen zu erwarten. Im Gegensatz zu den meisten Species der Cyprinidae und Characiformes ist es gewöhnlich schwierig, die Schreckreaktion für die Siluroidei nachzuweisen (Pfeiffer, 1960, 1963a, 1967). Schutz (1956) erzielte an *Ameiurus nebulosus* acht und an *Corydoras paleatus* zwei positive Ergebnisse, ohne sie als Schreckreaktion zu deuten, trotz seines Hinweises, daß diese Welse als Jungfische in Gruppen leben. Pfeiffer (1960) bestätigte die von Schutz (1956) an *Ameiurus* und *Corydoras* erhobenen positiven Befunde und wies die Schreckreaktion der Welse erstmalig an dem schwarmbildenden, tagaktiven Glaswels *Kryptopterus bicirrhis* (Siluridae) nach. Seitdem wurde die Schreckreaktion dieser und weiterer Species (*Pangasius sutchi* - Pangasiidae, *Eutropiellus vandeweyeri* - Schilbeidae und dem marinen *Plotosus lineatus* - Plotosidae) videotechnisch analysiert (Pfeiffer *et al.* 1986, Heyd & Pfeiffer, in Vorbereitung). Positive Ergebnisse liegen ferner für Angehörige der Mochokidae und Pimelodidae vor (Pfeiffer, 1963a).

Eine völlig andere Möglichkeit des Schutzes ist die Abschreckung des Angreifers, beispielsweise akustisch durch Stridulationslaute oder Knarren. Sie ist hauptsächlich bei solitären, wehrhaften Species zu erwarten, wie den stacheltragenden, meist nachtaktiven Welsen. Es war daher naheliegend zu prüfen, ob bei Welsen ein Zusammenhang zwischen Lauterzeugung und Schreckreaktion besteht, wie von Pfeiffer & Eisenberg (1965) vermutet. Trotz zahlreicher Sammelreferate über die Schreckreaktion einerseits (Pfeiffer, 1962b, 1963b, 1966, 1974, 1977, 1982; Smith, 1977, 1982, 1986, 1992; Solomon, 1977; Liley, 1982; Stabell, 1996) und die Lauterzeugung andererseits (Harden-Jones & Marshall, 1953; Tavolga, 1960, 1971a, 1977; Schneider, 1961, 1967; Winn, 1964; Popper & Fay, 1973, 1993; Fine *et al.*, 1977; Hawkins & Myrberg, 1983; Bass, 1989; Schellart & Wubbels, 1998; Tyack, 1998) wurde dieser Frage bisher keine Aufmerksamkeit geschenkt. Da sich die bisherigen Untersuchungen auf nur wenige Arten und Familien beschränken, haben wir weitere Species bezüglich ihrer Fähigkeit zur Lauterzeugung und deren Mechanismen studiert.

MATERIAL UND METHODEN

Bezüglich ihrer Lauterzeugung wurden 19 Species aus 8 Familien der Welse untersucht (Tabelle 1). Die Fische wurden als Jungtiere vom Großhandel bezogen; alle waren Wildfänge, ausgenommen *Corydoras paleatus*. Sie wurden in 200L-

Aquarien in Leitungswasser bei 24 - 26 °C Wassertemperatur gehältert (LD 12:12). Die Fütterung erfolgte je nach Species 1-2 mal täglich mit Flockenfutter, Futtertabletten, roten Mückenlarven (Frostfutter) und Rinderherz.

LAUTERZEUGUNG DURCH STRIDULATION:

Die Versuche begannen nach 6 Wochen Quarantänezeit und fanden in einem ruhigen Raum statt. Die Welse wurden nach einer Eingewöhnungszeit von etwa einer Stunde aus einem kleinen Transportaquarium gefischt, an einer Brustflosse und am Körper gefaßt und in 5-10 cm Abstand vor ein Mikrophon (Uher M 517) gehalten. Die bei Bewegung der freien Brustflosse erzeugten Laute wurden mit einem Tonbandgerät (Uher report stereo) bei 19 cm/sec Bandgeschwindigkeit aufgezeichnet. Die einzelnen Fische wurden am selben Tag höchstens zweimal aus dem Aquarium genommen, wobei eine mindestens halbstündige Pause eingehalten wurde. Wenn ein Wels keine Laute erzeugte, wurde er später zu unterschiedlichen Tageszeiten, auch am Abend, wieder geprüft.

Mittels eines Sonagraphen wurden von den Tonbandaufnahmen Sonagramme erstellt (Sonagraph Typ 6061, Papier Type B/65 Sonagram, Kay Elemetrics Corp., Pine Brook, NJ, USA), wobei die Registrierdauer 1,2 Sekunden im Frequenzbereich 160-16000 Hz betrug. Durch Darstellung der Intensitätsverteilung konnte eine Frequenzanalyse der Laute durchgeführt werden. Die Tonbandaufnahmen wurden möglichst vollständig in Sonagramme übersetzt, aus denen die Längen der Laute und der Intervalle (Pausen zwischen den Lauten) bestimmt und in Millisekunden (ms) umgerechnet wurden. Die Meßwerte für jedes Individuum und für die Summe aller Angehörigen derselben Species wurden statistisch bearbeitet. Dabei wurde innerhalb derselben Art nicht zwischen Ab- und Adduktionslauten unterschieden. Ferner konnte durch Abspielen der Tonbänder mit reduzierter Geschwindigkeit die Anzahl der registrierten Laute bestimmt werden. Der Quotient aus Lautanzahl und zugehöriger Aufnahmedauer ergibt ein relatives Maß für die Aktivität (den Erregungsgrad) des Versuchsfisches.

LAUTERZEUGUNG DURCH SCHWIMMBLASENMECHANISMEN:

Zur Lautaufnahme wurden die folgenden Geräte eingesetzt: Panasonic NV-FS 200 (SVHS-Videorecorder mit Long-Play-Aufnahmemöglichkeit); Videocassetten: Sony VHS E-240; Dyn. Mikrophon Vivanco- DM 22 (Frequenzbereich 60-12000 Hz, Impedanz 600 Ohm, Nierencharakteristik). Für die Unterwasseraufnahmen war dem Mikrophon ein Gefrierbeutel übergestülpt und wasserdicht abgeklebt. Dadurch wurden die eingegebenen Frequenzen weder an Luft noch unter Wasser beeinflußt, wie der folgende Versuch gezeigt hat: mit einem Frequenzgeber (SINE/SQUAR Oscillator Li Interlab SQ 10 mit einem 50 Ohm/0,2 Watt Lautsprecher) wurden definierte Töne erzeugt und über das Mikrophon unverpackt oder verpackt registriert. Diese Aufnahmen wurden mit einem Frequenzzähler bzw. Frequenzanalyse-PC-Programm (SONA-PC, B. Waldmann, Zoologisches Institut der Universität Tübingen) analysiert. Die Frequenz war stabil, das Mikrophon zeigte eine Richtcharakteristik. Mit

zunehmender Entfernung vom Mikrophonkopf sank die Intensität der Töne, abhängig von der jeweiligen Frequenz. Die Versuche wurden unter den folgenden Bedingungen durchgeführt: Aquariengröße 80x50x50 cm, Wassertemperatur 27-28°C, Lichtphase 7-19 Uhr (Leuchtstoffröhre); Fütterung 1x täglich am Vormittag. Die Fische wurden jeweils eine Woche eingewöhnt.

Versuch A: Zur Bestimmung der Tag-Nacht-Lautaktivität wurde im Abstand von drei Wochen an zwei verschiedenen Gruppen aus je 4 Exemplaren von *Arius seemani* (Gesamtlänge 205-240 mm) die Lautaktivität drei Tage (72 Stunden) lang ohne Unterbrechung auf Videoband registriert. Der Aquarienraum wurde nur zum Programmieren des Recorders, Wechseln der Cassetten und zur Fütterung betreten, um die Welse so selten wie möglich zu beunruhigen. Zur Bestimmung der Lautaktivität wurden die Bandaufnahmen abgehört, wobei von jeder Stunde drei 5-Minuten-Abschnitte ausgewählt und jeweils die Laute gezählt wurden. Aus diesen an den drei Aufnahmetagen immer zur selben Stunde ermittelten Werten (n = 9) wurde der Median berechnet (= mittlere Lautaktivität in 5 Minuten). Dieser wurde mit 12 multipliziert und dient als geschätztes Maß für die Lautaktivität während der betreffenden Stunde.

Versuch B: Nach Abschluß der beiden Langzeitversuche wurden nachmittags drei Welse aus der zweiten Gruppe entnommen und die Laute des im Aquarium verbliebenen Individuums sofort nach dieser Störung bzw. nach einer Beruhigungsphase von 15 Minuten registriert. Von diesen Aufnahmen wurden jeweils 20 Laute mit dem Sona-PC-Programm in bezug auf Frequenzanteile (Fourier-Analyse) sowie Laut- und Intervalldauer ausgewertet.

Für die vergleichend-morphologischen Untersuchungen dienten je 3 *Arius seemani* (215-260 mm Gesamtlänge), *Pimelodus pictus* (105-110 mm) und *Pimelodella gracilis* (110-125 mm). Von jeder Species wurden nach Tötung mit MS 222 (Sigma Chemical Co.) ein Exemplar frisch präpariert und zwei in Formalin (1:10 verdünnt) fixiert. Alle Fische wurden ventral geöffnet und geprüft auf den Besitz eines Fensters in der Muskulatur jeder Körperseite ("the lateral cutaneous areas": Bridge & Haddon, 1893; Alexander, 1964, 1965, 1966). Ferner wurden Lage, Größe und Form ihrer Schwimmblase notiert. Schließlich wurde nach einem Trommelmuskelapparat gesucht. Während der Präparation wurde mit einer ZEISS-Aufsetzkamera M 35 am ZEISS-Standardbinokular fotographiert (Filmmaterial: Agfa HDC 100/21, Fujichrome 50/18, Kodak 100/21).

ERGEBNISSE

STRIDULATION

Alle Species reagierten auf Berührung mit Zappeln, Schwanzschlagen, Aufrichten der Rückenflosse sowie mit Abspreizen und Arretieren oder Bewegungen der Brustflossen. Bei letzterem erzeugten 13 der 18 untersuchten Species Stridulationslaute (Tab. 1, 2). Am lautesten waren die beiden *Synodontis*-Species, *Agamyxis* und *Glyptoperichthys*, während *Peckoltia* besonders leise stridulierte. Die Angehörigen derselben Art waren unterschiedlich erregt: die einen begannen schon beim Herausfischen zu stridulieren, die anderen erst beim Anfassen, einige blieben auch bei

TABELLE 1

Familienzugehörigkeit der 19 untersuchten Welsarten, in Tab. 2 und Abb. 6-9 verwendete Abkürzungen (Abk.), Anzahl der auf Stridulation geprüften Exemplare (N) und deren Gesamtlänge.
* es könnte sich um *Peckoltia vittata* (Steindachner, 1882) handeln.
** Syn. *Pimelodella meesi*. *** nur auf Trommelmechanismen untersucht.

Familie / Species	**Abk.**	**N**	**Länge (mm)**
Ariidae			
Arius seemani Günther, 1864	As	12	60-85
Aspredinidae			
Dysichthys coracoideus Cope, 1874	Dc	5	80-100
Bagridae			
Hemibagrus nemurus (Valenciennes, 1839)		4	110-122
Mystus gulio (Hamilton, 1822)	Mg	4	63-67
Mystus vittatus (Bloch, 1794)	Mv	3	55-62
Callichthyidae			
Corydoras paleatus (Jenyns, 1842)		13	40-50
Dianema urostriata De Miranda-Ribeiro, 1912	Du	5	40-55
Doradidae			
Agamyxis flavopictus (Steindachner, 1908)	Af	3	53-65
Loricariidae			
Ancistrus cf. *dolichopterus* Kner, 1854		3	55-70
Glyptoperichthys gibbiceps (Kner, 1854)	Gg	3	100-120
Panaque nigrolineatus (Peters, 1877)		2	55-60
Parancistrus aurantiacus (Castelnau, 1855)		1	80
Peckoltia pulcher (Steindachner, 1915) *	Pp	3	73-90
Pseudacanthicus spinosus (Castelnau, 1855)		3	70-95
Mochokidae			
Synodontis ocellifer Boulenger, 1900	So	3	105-130
Synodontis schoutedeni David, 1936	Ss	3	80-100
Pimelodidae			
Brachyrhamdia meesi Sands & Black, 1985**	Bm	1	70
Pimelodella gracilis *** (Cuvier & Valenciennes, 1840)		-	-
Pimelodus pictus Steindachner, 1876		4	75-90

wiederholtem Fangen ruhig. Eine hohe Stridulationsaktivität zeigten die beiden *Mystus*- und *Synodontis*-Arten sowie *Agamyxis flavopictus* und *Peckoltia pulcher* (Tab. 2). Der Erregungsgrad aller untersuchten Individuen lag im Durchschnitt zwischen 0,9 und 2,5 Lauten pro Sekunde. Nur bei 5 Species stridulierten alle Individuen; von 66 stridulierfähigen Individuen aller Species blieben 24 (36%) auch bei wiederholten Störungen stumm (Tab. 2). Stridulation im Wasser trat nur selten auf. Einmal lärmte ein *Agamyxis* im Aquarium, als er mit zwei Artgenossen in die Quere kam. Ein *Pimelodus* stridulierte im Becherglas, mit dem er aus dem Aquarium genommen worden war. *Dysichthys* beantwortete das Anfassen im Wasser mit Körpervibrationen.

TABELLE 2

Ergebnisse der Untersuchungen zur Stridulation (Abkürzungen der Speciesnamen vgl. Tabelle 1). Nur stridulierende Species sind hier aufgelistet.
S: Stridulationsweise (Ab = Abduktion, Ad = Adduktion).
n (N): Anzahl n der stridulierenden Individuen von allen geprüften Exemplaren (N) einer Species; E: Erregungsgrad (Anzahl Laute / sec., Mittelwerte ± Standardabweichung); L: Lautdauer (Medianwerte) in ms; P: Intervalldauer (Medianwerte) in ms; F: Frequenzschwerpunkte der Laute in kHz.

Species	**S**	**n (N)**	**E**	**L**	**P**	**F**
As	Ab	6 (12)	1.1 ± 0.5	30.2	77.4	1-3; 4-5; 10-11
Bm	Ab	1 (1)	0.9	52.8	75.5	2-4; 6-8
Du	Ab	3 (5)	1.0 ± 0.6	41.5	71.7	0.5-2; 3-4
Gg	Ab	3 (3)	1.1 ± 0.7	77.55	230.2	1.5-2.5; 4-5
Pp	Ab	3 (3)	1.6 ± 0.6	67.9	130.2	4-6; 9-12
Af	Ab+Ad	3 (3)	1.4 ± 0.4	101.9	56.6	2-3; 5-6
Dc	Ab+Ad	4 (5)	1.1 ± 0.6	83.95	41.5	0.5-2
Mg	Ab+Ad	3 (4)	1.4 ± 1.2	45.3	34	3-4; 7-8
Mv	Ab+Ad	3 (3)	1.4 ± 0.4	34.9	34	3-5; 8-10
So	Ab+Ad	2 (3)	1.3 ± 1.6	61.35	15.1	1-2; 3.5-4.5
Ss	Ab+Ad	2 (3)	2.5 ± 1.3	49.1	23.55	0.5-2

Die Stridulationslaute entstanden je nach Species auf unterschiedliche Weise. Während *Arius*, *Brachyrhamdia*, *Dianema*, *Glyptoperichthys* und *Peckoltia nur* bei Abduktion (Abspreizen) der Brustflosse Laute erzeugten, geschah dies bei *Agamyxis*, *Dysichthys*, den *Mystus*- und den *Synodontis*-Arten bei Abduktion *und* Adduktion (Heranziehen) der Brustflosse (Tab. 2). Lauterzeugung *nur* bei Adduktion wurde nie beobachtet. Die Geräusche bestehen aus Serien einzelner Laute, welche wiederum aus Einzelknacks aufgebaut sind, die bei kürzeren Lauten dichter aufeinander folgen als bei längeren. Diese Einzelknacks sind bei Arten mit Abduktionslauten ziemlich gleichmäßig angeordnet und die Laute einer Serie ähnlich gestaltet (Abb. 1, 2). Teilweise können anhand der Sonagramme die Abduktionslaute von den Adduktionslauten an ihrer unterschiedlichen Dauer bzw. der Dichte der Einzelknacks unterschieden werden (Abb. 3, 4, 5). Die Laute zeigen keinen harmonischen Aufbau, sondern eine breite Frequenzverteilung. Die Bereiche größter Energie sind in den Sonagrammen an den stark geschwärzten Stellen (Banden) erkennbar (Abb. 1-5). Oft treten zwei oder drei Banden auf, wobei die niedrigste Frequenz den Hauptbereich darstellt. Die Hauptfrequenzanteile liegen bei 500 - 6000 Hz (Tab. 2).

Aufgrund individueller Unterschiede (Abb. 6) ergeben sich in der Zusammenfassung für jede Species teilweise große Schwankungen der Laut- und noch mehr der Pausenlängen (Abb. 7). Kurze Laute im Bereich bis 50 ms erzeugen *Arius*, *Dianema*, *Mystus gulio*, *M. vittatus* sowie *Synodontis schoutedeni*. Bei den restlichen Species betragen die mittleren Lautlängen 50 - 100 ms (Tab. 2). Die größte Variabilität der Lautlänge zeigen *Agamyxis*, *Dysichthys*, *Glyptoperichthys* und *Peckoltia*, wobei einzelne Laute mehr als 150 ms dauern. Auch das einzige Exemplar von *Brachyrhamdia*

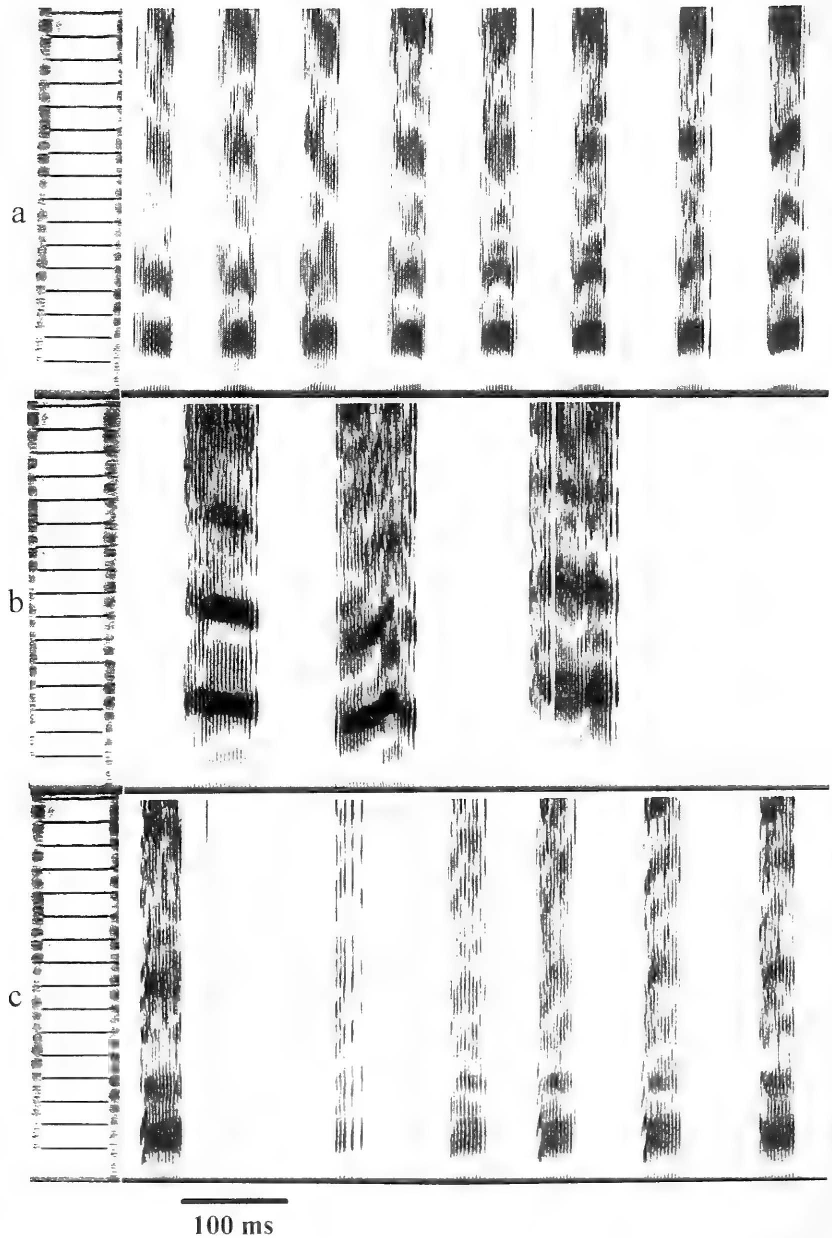


Abb. 1

Ausschnitt je eines Sonagramms von: a) *Arius seemani*, b) *Brachyrhamdia meesi*, c) *Dianema urostriata*. Abszisse: Zeitskala in ms. Ordinate: Frequenzskala 0-16 kHz in 1-kHz-Stufen.

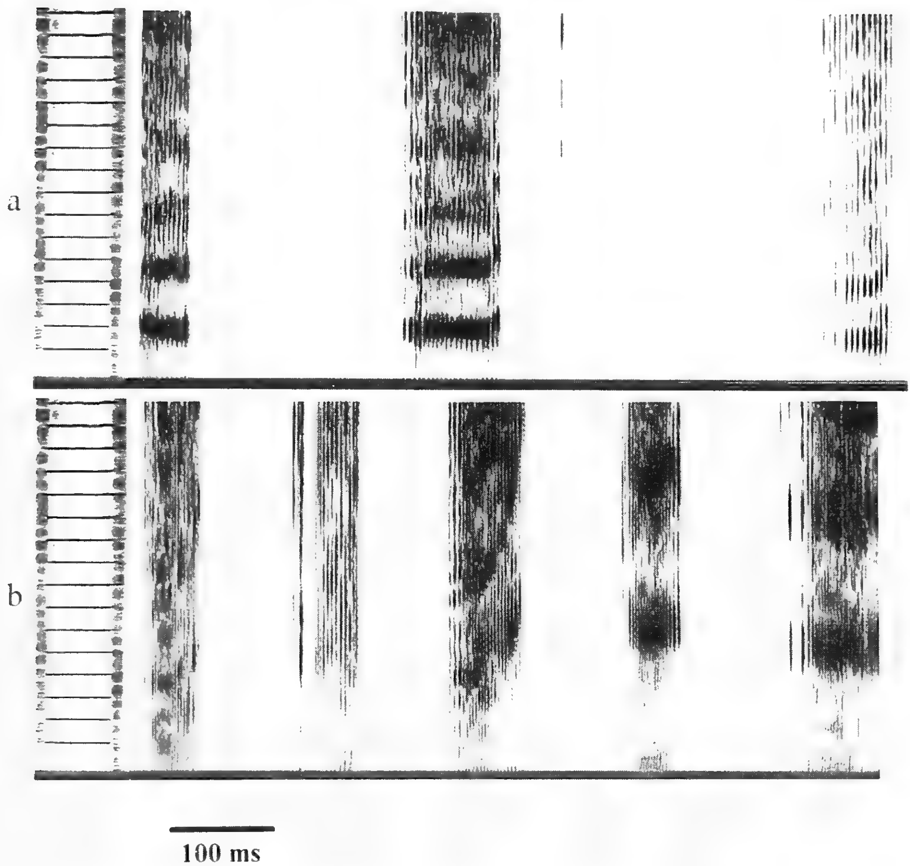


ABB. 2

Ausschnitt je eines Sonagramms von: a) *Glyptoperichthys gibbiceps*, b) *Peckoltia pulcher*. Achsen wie in Abb. 1.

weist bei kürzerer Lautdauer eine große Streuung auf (Abb. 7a). Die Pausenlänge ist am geringsten und streut am wenigsten bei den zwei *Synodontis*-Arten und *Mystus vittatus*; sie ist am größten bei *Glyptoperichthys* und streut am breitesten bei *Dianema* und *Dysichthys* (Abb. 7b).

Während ein Zusammenhang zwischen Erregungsgrad und Laut- bzw. Pausenlängen nicht ersichtlich ist (Tab. 2), zeigt sich im Verhältnis von Lautlänge zu Pausenlänge eine Abhängigkeit von der Art der Lauterzeugung (Abb. 8). Bei Species, die Ab- und Adduktionslaute erzeugen, sind die Laute mindestens ebenso lang wie die Pausen (Verhältnis meist größer als 1); bei Species mit Abduktionslauten übersteigt die Intervalldauer die Lautdauer teilweise weit (Verhältnis kleiner als 1).

a

b

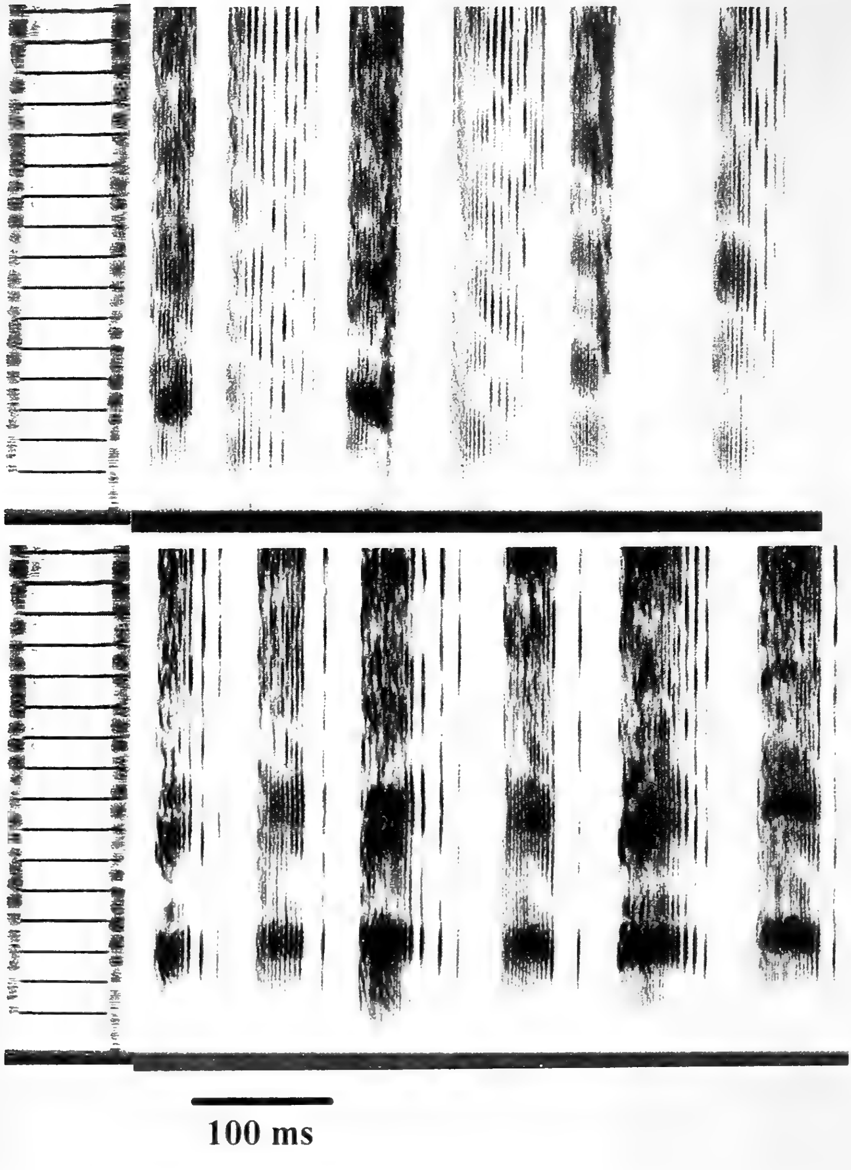


ABB. 3

Ausschnitt je eines Sonagramms von: a) *Mystus gulio*, b) *Mystus vittatus*. Achsen wie in Abb. 1.

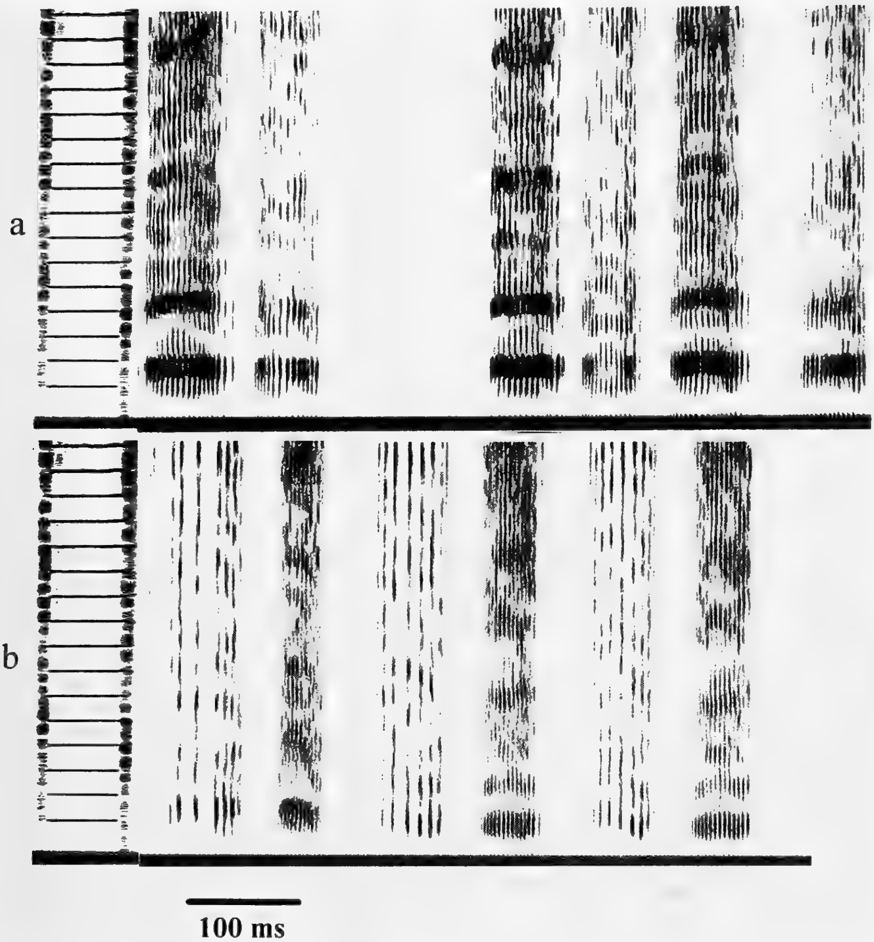


ABB. 4
Ausschnitt je eines Sonagramms von: a) *Synodontis ocellifer*, b) *Synodontis schoutedeni*. Achsen wie in Abb. 1.

Der Panzerwels *Corydoras paleatus* erzeugte Stridulationslaute auf folgende Art und Weise: wurde der Hinterkörper beidseitig gefaßt, warf der Fisch seinen Vorderkörper schnell hin und her. Dabei waren Laute hörbar, deren Sonagramme Stridulationslauten ähneln (Abb.9). Wurde der Fisch am Rumpf und an einer Brustflosse festgehalten, blieb die andere Pectoralis arretiert. Im Gegensatz zur stridulierenden *Peckoltia* zeigten die Loricariidae *Ancistrus* cf. *dolichopterus*, *Panaque nigrolineatus*, *Parancistrus aurantiacus* und *Pseudacanthicus spinosus* aus derselben Unterfamilie Ancistrinae zu keiner Tageszeit Stridulation. Alle Individuen dieser

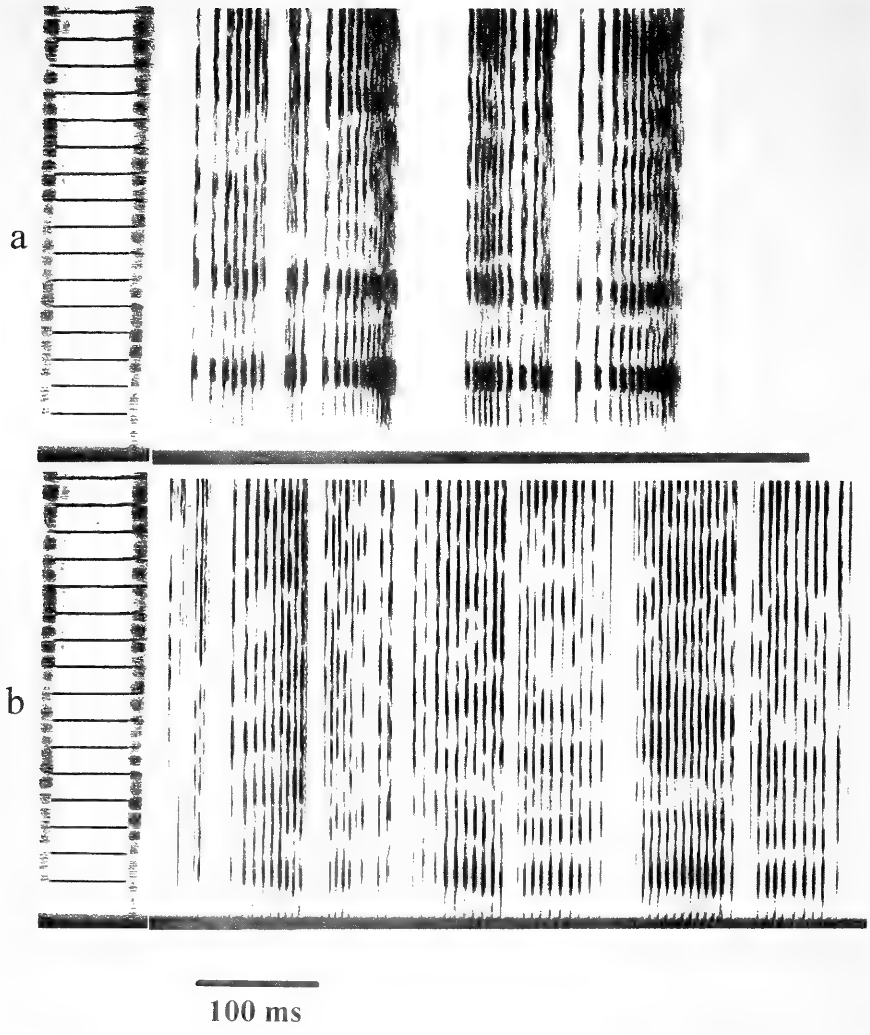


ABB. 5
Ausschnitt je eines Sonagramms von: a) *Agamyxis flavopictus*, b) *Dysichthys coracoideus*. Achsen wie in Abb. 1.

Species, ausgenommen *Peckoltia*, verhielten sich beim Herausnehmen aus dem Wasser ähnlich. Sie spreizten und arretierten beide Brustflossen, richteten ihre Rückenflosse auf und führten Schwanzschläge aus. Im Gegensatz zu *Pseudacanthicus* klappten *Ancistrus* und *Parancistrus* zusätzlich ihre mit Hakenstacheln besetzten Interopercula nach außen. *Panaque* besitzt keine solchen Interopercula. Anders als die

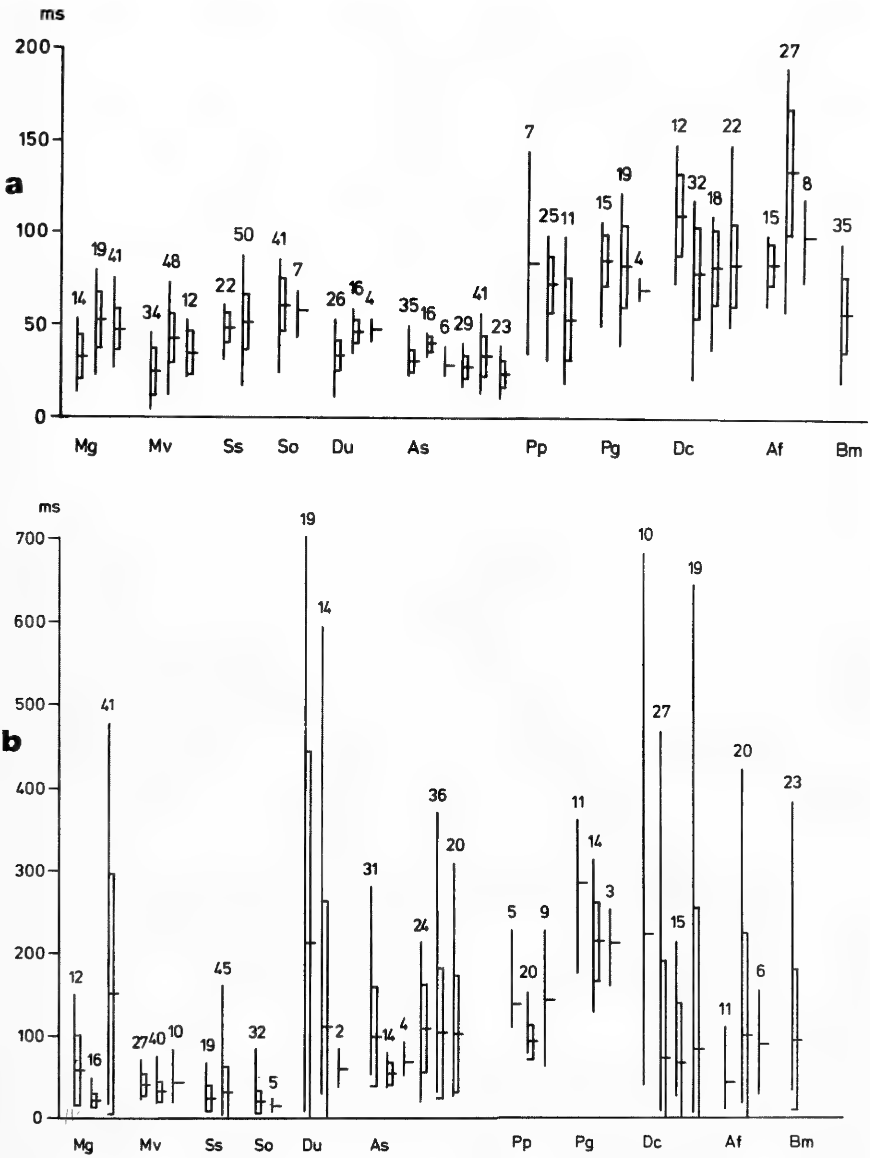


ABB. 6

Dauer der Stridulationslaute (a) und der Pausen zwischen den Lauten (b) von 33 Individuen aus 11 Species. Dargestellt sind Mittelwert, Standardabweichung, Minimum und Maximum sowie Anzahl der Laute (Ziffer). Abszisse: Species (Abkürzungen siehe Tab. 2; Pg = *Pterygoplichthys gibbiceps* = Synonym von *Glyptoperichthys gibbiceps* = Gg). Ordinate: Dauer in ms. Beachte die stärkere Dehnung der Ordinate in (a) gegenüber (b).

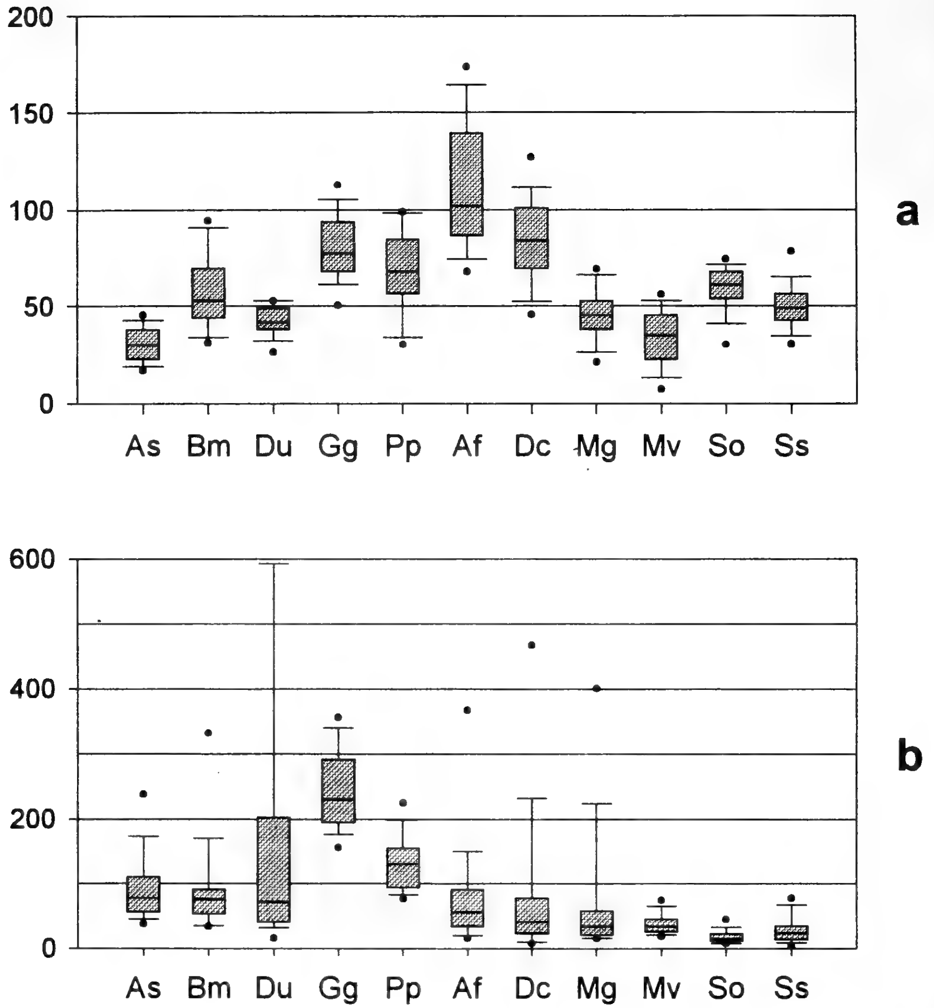


ABB. 7

Box-whisker-plots der Lautdauer (a) und der Pausendauer (b) der 11 Species. Abszisse: Species in Reihenfolge nach der Stridulationsweise: As-Pp Abduktion; Af-Ss Ab- und Adduktion. Abkürzungen siehe Tab. 2. Ordinate: Dauer in ms. Box: Median, 25. und 75. Perzentil. Whisker: 10. und 90. Perzentil. Punkte: 5. und 95. Perzentil.

beiden Bagridae der Gattung *Mystus* stridulierten vier wiederholt geprüfte Exemplare von *Hemibagrus nemurus* nicht, zeigten jedoch ein anderes bemerkenswertes Verhalten. Sie erzeugten mehrmals hintereinander durch Auspressen von Luft aus ihren Kiemenspalten Quietschlaute von 26 - 56 ms Dauer, mit einer Hauptfrequenz von 1,5 kHz (Abb. 10). Bei *Pimelodus pictus* waren wenige Stridulationslaute gleichzeitig mit Trommelmuskellauten zu hören.

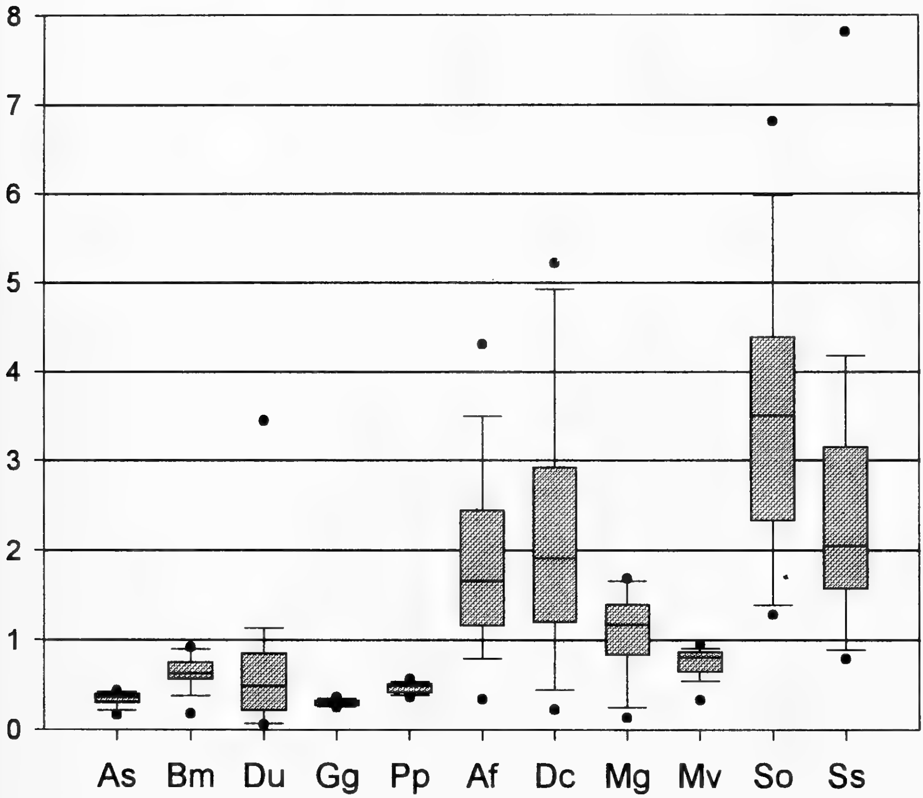


ABB. 8
Verhältnis von Lautdauer zu Pausendauer für jede Species, dargestellt als box-whisker-plots. Erläuterung siehe Abb. 8.

TROMMELMECHANISMEN:

Pimelodus pictus: alle vier Individuen erzeugten Laute, die an das Summen einer Fliege oder Hummel erinnern. Ein Exemplar stridulierte kurz außerhalb des Wassers, wobei gleichzeitig das Summen ertönte. Auch ein im Becherglas stridulierendes Exemplar summte. Die Summtöne waren etwa 1 sec lang und wurden mehrmals hintereinander erzeugt.

Arius seemani: beim Transport dieser Welse waren ebenso wie im Aquarium Laute vernehmbar, die sich wie „Popps" anhörten und entfernt an das Gackern von Hühnern erinnerten. Auf Klopfen an das Aquarium stellten die Fische diese Geräusche für einige Sekunden ein. Manche Individuen ließen diese Laute auch außerhalb des Wassers hören, während sie gleichzeitig stridulierten. Diese Laute waren leiser als das durch Stridulieren erzeugte Knarren.

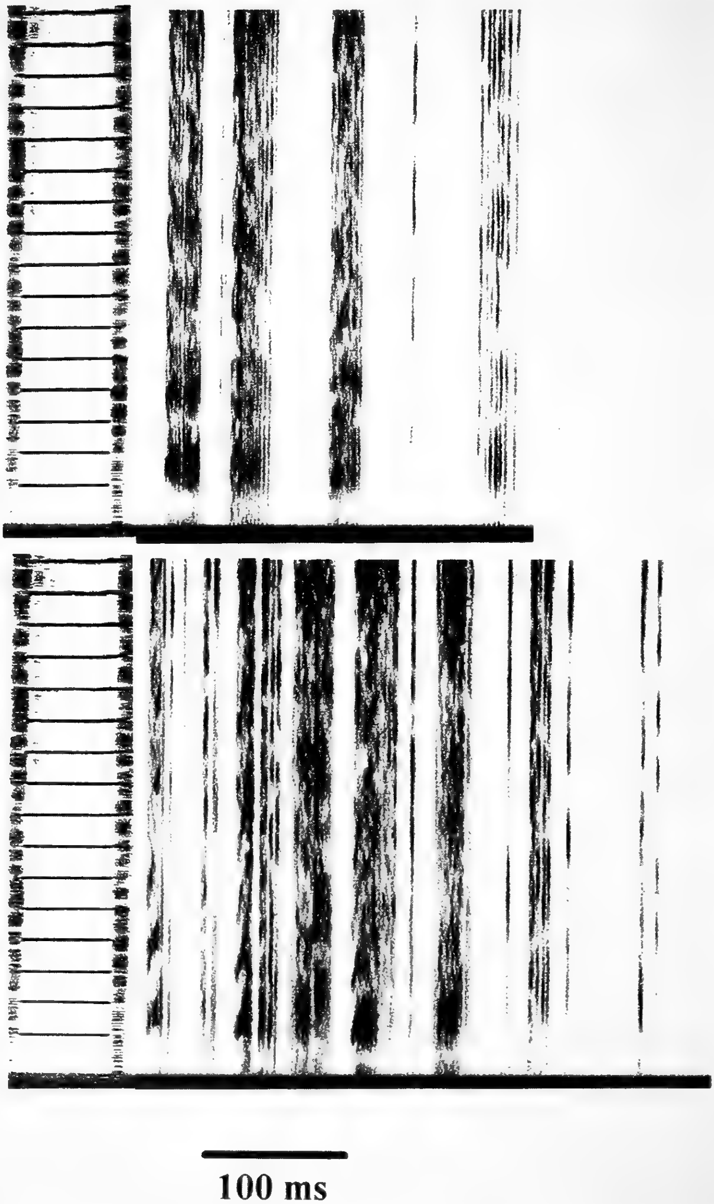


ABB. 9
Ausschnitte aus Sonagrammen von *Corydoras paleatus* (2 Exemplare). Achsen wie in Abb. 1.

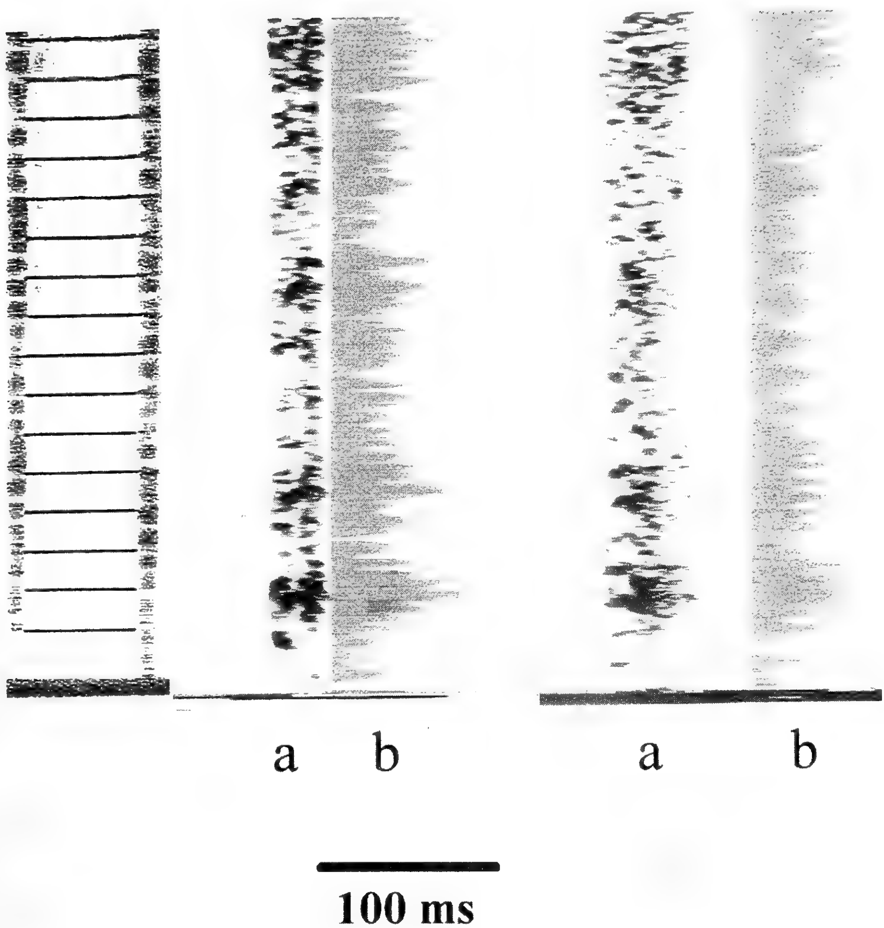


ABB. 10

Zwei "Quietschlaute" eines Exemplars von *Hemibagrus nemurus*. a: Sonagramm. b: Frequenzanalyse des Sonagraphen; vertikal Frequenz, horizontal Amplitude.

Versuch A: Die 4 Fische der ersten Gruppe begannen gleich nach dem Einsetzen in das Versuchsaquarium Trommellaute zu erzeugen, die in 1 m Entfernung vom Aquarium zu hören waren. Tagsüber lagen diese Welse entweder eng beisammen ruhig am Boden oder ruhten mit dem Kopf nach oben fast senkrecht an einer Aquarienwand. Bei Fütterung schwammen sie umher, danach ruhten sie wieder beieinander. Auch die zweite Gruppe gab sofort nach dem Einsetzen ins Versuchsaquarium Trommellaute von sich. Sie verhielt sich insgesamt ruhiger als die erste

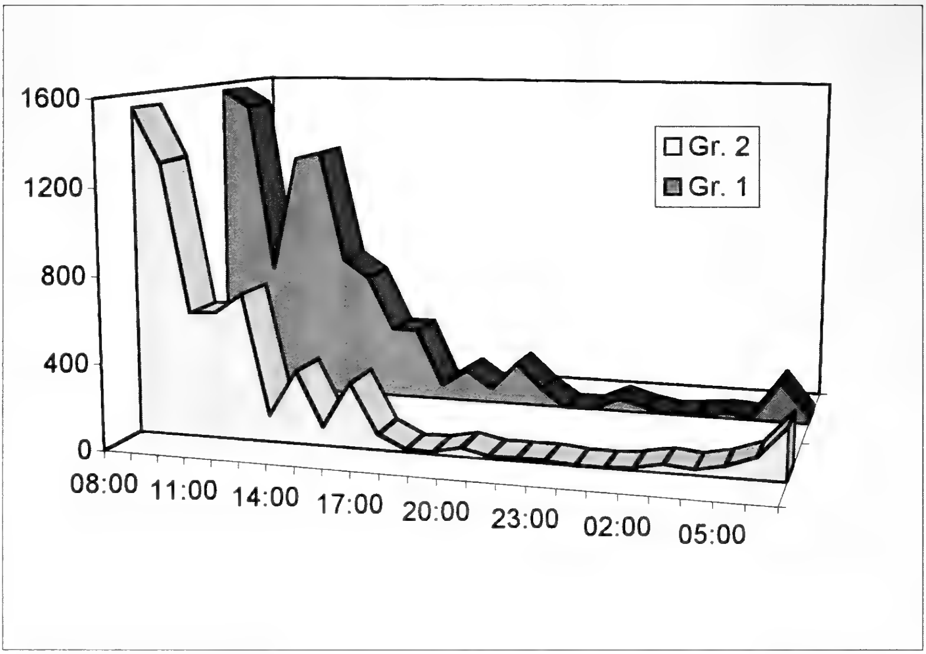


ABB. 11

24-Stunden-Lautaktivität der beiden Gruppen (Gr. 1, Gr. 2) von *Arius seemani*. Dargestellt sind Medianwerte über 3 Tage. Abszisse: Uhrzeit. Ordinate: Anzahl der Laute.

Gruppe und erzeugte bei Fütterung und beim Hantieren am Aquarium weniger Laute. Das Verhalten am Tag ähnelte dem der ersten Gruppe. Beide Gruppen zeigten in ihrer Lautaktivität einen ausgeprägten Tag-Nacht-Rhythmus (Abb. 11). Die Lautproduktion war am Tag deutlich höher als nachts und etwa 1 Stunde nach Einsetzen der Lichtperiode am höchsten. Die Lautaktivität nahm dann ab, um gegen 12 Uhr ein erneutes, aber kleineres Maximum zu erreichen. Am Nachmittag war ein weiteres, schrittweises Abklingen der Lautanzahl zu verzeichnen. Zwischen 19 und 7 Uhr (Dunkelphase) erzeugten die Welse nur wenige Laute. Bereits zwei Stunden vor der Lichtperiode (7 Uhr) intensivierten beide Gruppen ihre Lautaktivität. Die Lautserien waren am Morgen gehäuft, am Mittag vereinzelt und wurden oft nur von einem einzigen Fisch erzeugt. Die nachts registrierten Laute waren dagegen meist Einzelgeräusche, nur ausnahmsweise Serien. Bei Gruppe 1 war die Gesamtzahl der Laute in der Hellphase um etwa 50 %, nachts um etwa 23 % höher als bei Gruppe 2.

Versuch B: Alle Laute des isolierten Exemplars zeigten gleiche Frequenzspektren. Die Hauptfrequenzen lagen unter 500 Hz. Die maximale Intensität war bei 140 - 200 Hz, hohe Intensitäten sind bei 250 - 400 Hz zu erkennen (Abb. 12). Die mittlere Lautdauer betrug 209,5 ± 17,4 ms, die Intervalldauer 0,3 - 6 sec.

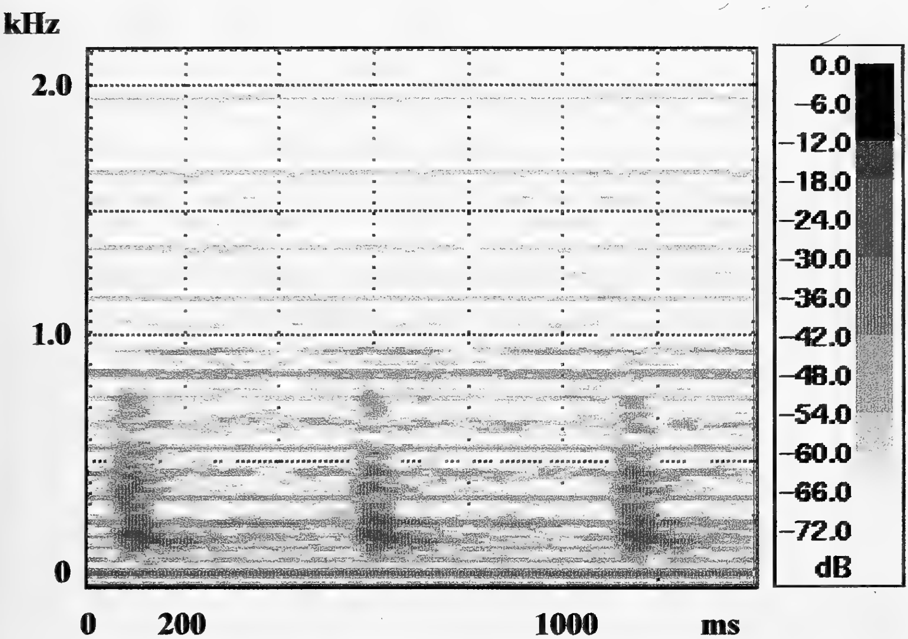


ABB. 12

Farbspektrogramm der Trommellaute von *Arius seemani*. Abszisse: Zeitachse in ms. Ordinate: Frequenz in kHz. Farbskala rechts: Intensitätsverteilung des Schalldruckpegels in dB.

Struktur der Trommelmuskelapparate (Schwimmblasenmechanismen):

Arius seemani besitzt im Bereich der vorderen Schwimmblasenkammer, ein laterales Fenster in der Muskulatur ("lateral cutaneous area"). Die Versteifung des Schädel-Hals-Bereiches wird durch den mit dem Basioccipitale fest verwachsenen Wirbelkomplex verstärkt. Eine knöcherne Lamelle des Epioticums ist mit dem Transversalfortsatz des 4. Wirbels fest verbunden. Der Wirbelkomplex wird von den Wirbeln 2 bis 7 gebildet. Die Wirbel 4 bis 7 formen mit ihren Transversalfortsätzen eine der Schwimmblase aufliegende Platte. Während die Transversalfortsätze 6 und 7 nur starres Bindegewebe miteinander verbindet, sind die Fortsätze 4 und 5 miteinander verwachsen. Der anteriore Teil des Transversalfortsatzes des 4. Wirbels ist zu einem langen, ventrad gebogenen Ast ausgezogen. Tavolga (1962) hat ihn zu Ehren seines Entdeckers Johannes Müller (1842) „Müller' sche Ramus" genannt (Abb. 13). Dieser lanzenförmige Ramus liegt der Schwimmblase craniad auf und ist mit ihr über Bindegewebe verwachsen, das ihn bis zum Ansatz des Trommelmuskels überzieht. Dieser indirekte Trommelmechanismus wurde von Müller (1842) als „Springfederapparat" („elastic spring apparatus") bezeichnet. Er wird vom Transversalfortsatz des 4. Wirbels, dem Müller'schen Ramus und dem Trommelmuskel (Protractor) gebildet. Der Protractor hat seinen Ursprung am Posttemporale, dem Epioticum und dessen knöcherner Lamelle. Die Ansatzstellen des Muskels liegen am Vorderrand des Transversalfortsatzes des 4. Wirbels bis zu dessen Verbindung mit

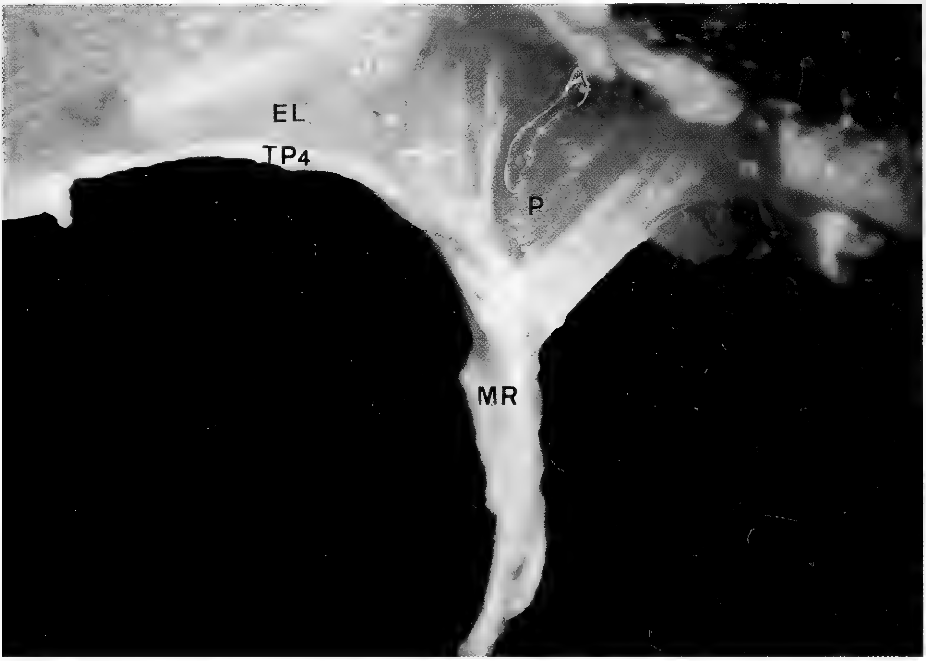


ABB. 13

Springfederapparat von *Arius seemani* (215 mm) der rechten Körperseite von lateral. P, Protractor mit blutrotem anterioren Anteil. El, knöcherne Lamelle des Epioticums. TP_4, Transversalfortsatz des 4. Wirbels. MR, Müller'sche Ramus. 8:1.

der Epioticum-Lamelle. Ein weiterer Teil des Muskels zieht zum proximalen Müller'schen Ramus. Der vordere Bereich des fächerförmigen Trommelmuskels erscheint am frischen Präparat stärker blutrot als der zum Transversalfortsatz des 4. Wirbels ziehende Ast. Beide Muskelbereiche lassen sich kaum voneinander trennen, da sie gemeinsam den Protractor bilden (Abb. 13). Die herzförmige Schwimmblase eines 260 mm großen *Arius* ist 33 mm lang und erstreckt sich bis zum 8. Wirbel, eingerahmt vom Müller'schen Ramus, dem Wirbelkomplex und dessen Transversalfortsätzen. Sie wird durch ein unvollständiges Diaphragma in eine anteriore und eine posteriore Kammer geteilt. Letztere wird durch zwei Transversalsepten weiter unterteilt. Die Ansatzstellen der Septen sind an der dorsalen und ventralen Schwimmblasenwand verbreitert (Abb. 14). Der kleine Ductus pneumaticus zieht vom caudalen Ende der vorderen Schwimmblasenkammer zum Vorderdarm.

Pimelodus pictus: Die vordere Schwimmblasenkammer grenzt teilweise an die Haut. Die Wirbelkörper 2 bis 5 sind miteinander verwachsen. Die Transversalfortsätze der Wirbel 4 und 5 bilden zusammen eine starre, der Schwimmblase aufliegende, leicht geschwungene Platte. Der Transversalfortsatz des 4. Wirbels teilt sich distal in einen anterioren und einen posterioren Ast, an dessen wulstartig verstärktem cranialem Rand der Trommelmuskel entspringt. Dieser Fortsatz ist gelenkig mit dem

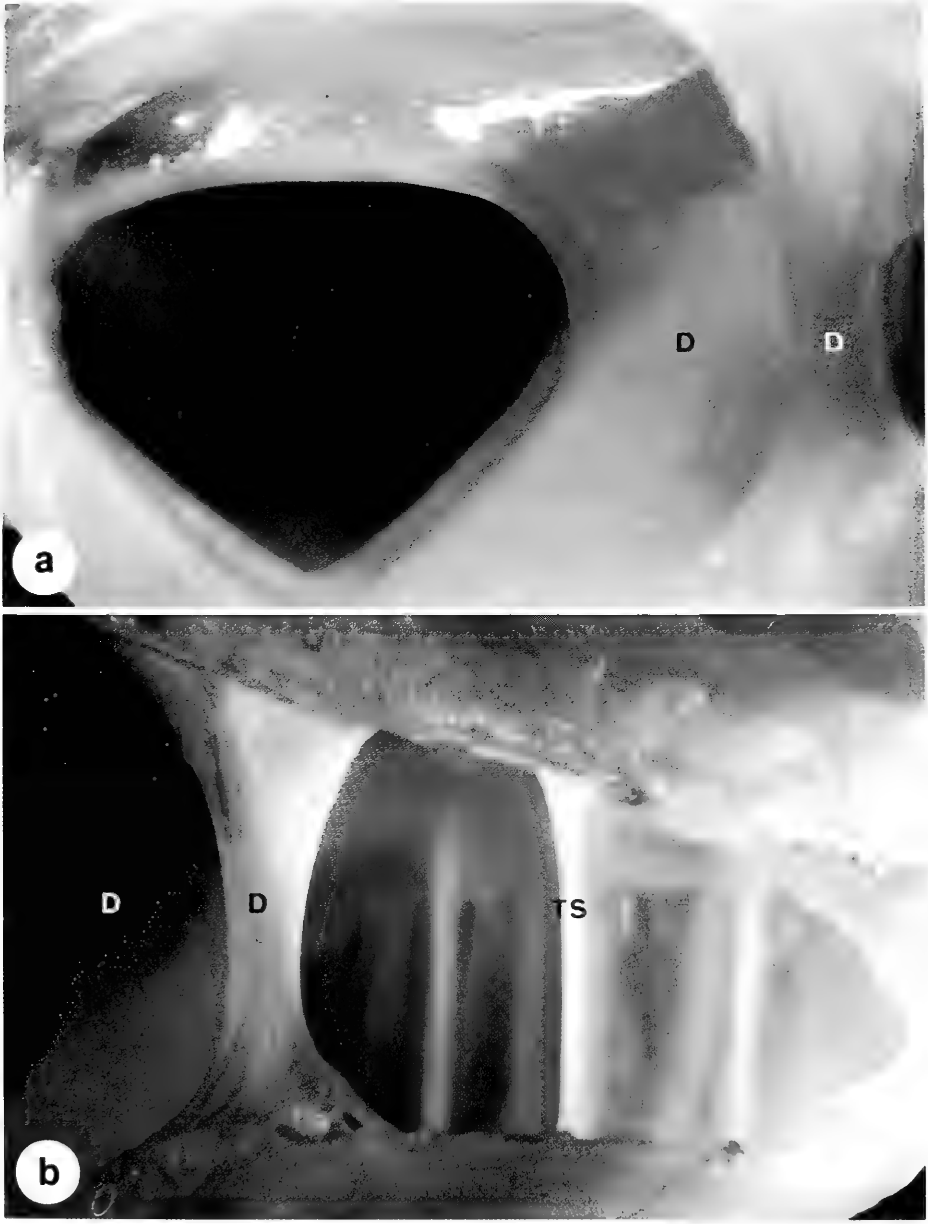


ABB. 14

Schwimmblase von *Arius seemani* (260 mm, männlich), linke Körperseite, lateral geöffnet. a) anteriore Kammer, durch das Diaphragma (D) von der posterioren Kammer teilweise getrennt. 8:1. b) posteriore Kammer. Deutlich sichtbar die Transversalsepten (TS) und das Diaphragma (D), das sich wie die TS and der dorsalen und ventralen Schwimmblasenwand verbreitert. 8:1.

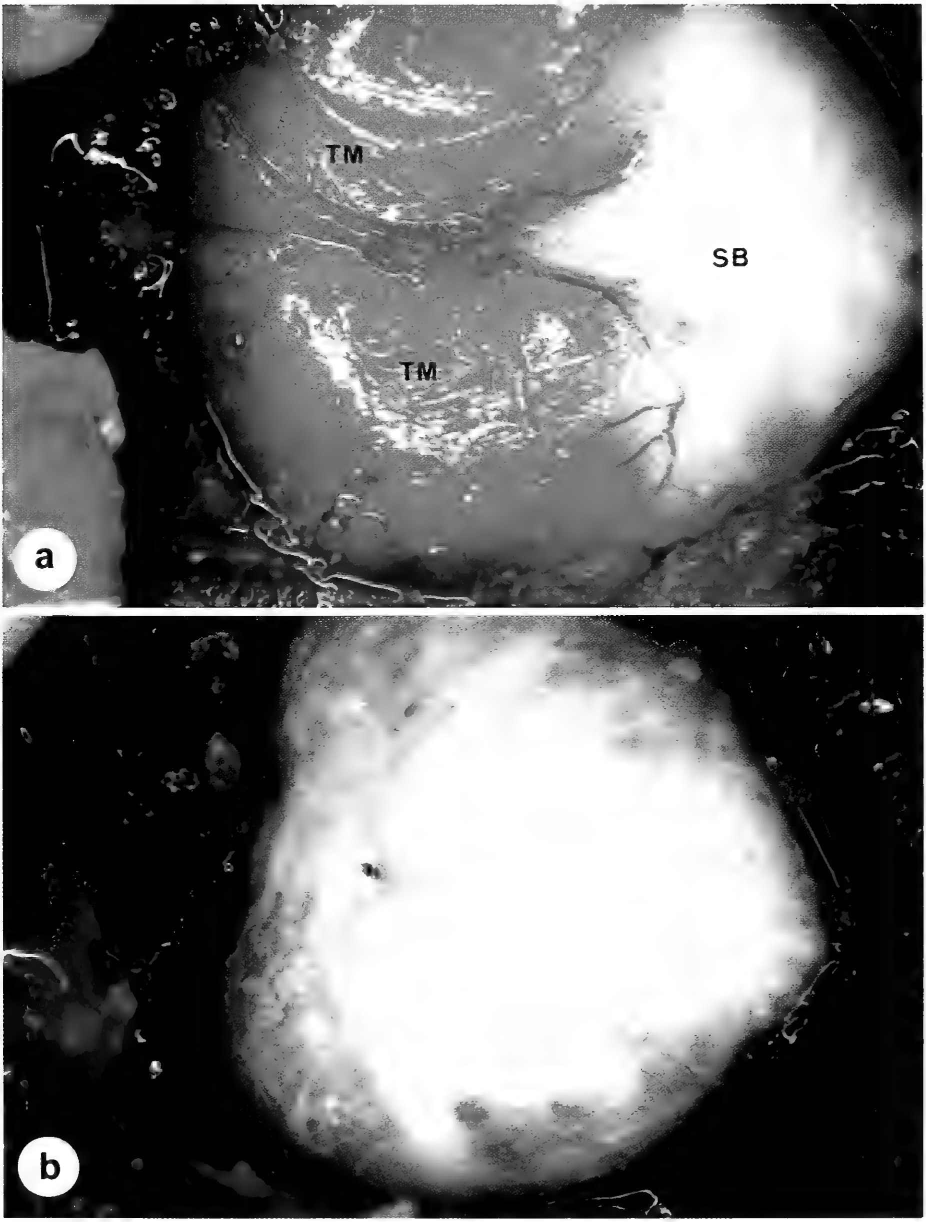
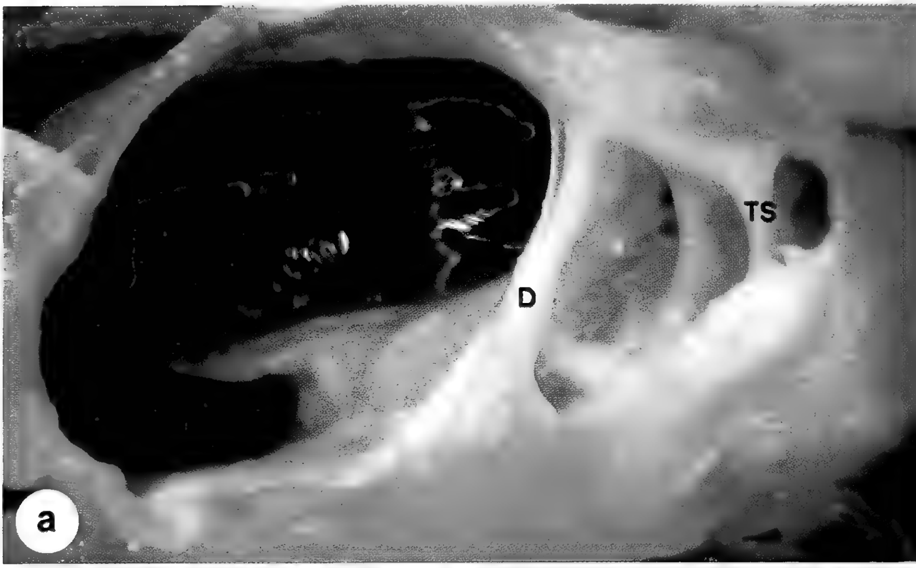


ABB. 15

Schwimmblasen von ventral. a) *Pimelodus pictus* (105 mm). Der blutrote Trommelmuskel (TM) überdeckt mehr als die Hälfte der Schwimmblase (SB). 8:1. b) *Pimelodella gracilis* (123 mm). Schwimmblase frei, kein Trommelmuskel. 8:1.



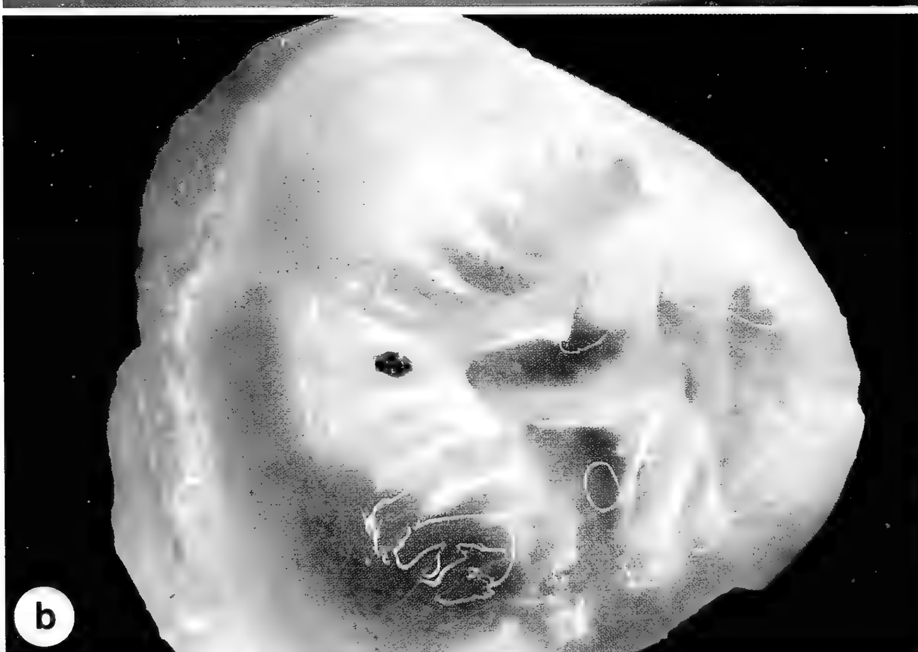


ABB. 16. *Pimelodus pictus* (Kopf nach links gelegen) a) Schwimmblase eines 105 mm langen Exemplars von links lateral geöffnet. Die anteriore großlumige Kammer ist von der posterioren Kammer durch ein Diaphragma (D) teilweise getrennt. Der hintere Schwimmblasenteil ist von Transversalsepten (TS) weiter unterteilt. 12:1. b) Schwimmblase eines 120 mm langen formalin-fixierten Exemplars, von dorsal geöffnet. Deutlich sind die zur dorsalen Schwimmblasenwand ziehenden Septen, die sich an ihren Ansatzstellen verbreitern. 8:1.

Posttemporale verbunden. Der paarige, durch große Blutgefäße versorgte und daher intensiv rote Trommelmuskel (Protractor) hat seinen Ursprung am Transversalfortsatz des 4. Wirbels und reicht über die Hälfte der ventralen Schwimmblasenwand. Er bedeckt die vordere Schwimmblasenkammer mit Ausnahme der "lateral cutaneous areas" und setzt am cranialen Ende der hinteren Kammer an. An seiner Ansatzstelle läuft der Trommelmuskel flach aus. Seine Ansatzareale sind S-förmig gekrümmt. Die herzförmige Schwimmblase erstreckt sich vom 2. bis zum 6. Wirbel und ist bei einem 105 mm großen Exemplar 15 mm lang (Abb. 15). Sie wird durch ein unvollständiges Diaphragma in eine anteriore und eine posteriore Kammer unterteilt. Weil das Diaphragma von lateral-dorsal gelegenen Öffnungen durchbrochen wird, sind die beiden Kammern miteinander verbunden. Die posteriore Kammer wird durch Transversalsepten nur unvollständig weiter unterteilt. Die Septenbildung beginnt an der Ansatzstelle des Trommelmuskels und reicht bis zum caudalen Schwimmblasenende. Die Septen ziehen zur dorsalen und ventralen Schwimmblasenwand (Abb. 16). Der Ductus pneumaticus entspringt in der Mitte des caudalen Endes der vorderen Schwimmblasenkammer.

Pimelodella gracilis besitzt ebenso wie *Pimelodus pictus* und *Arius seemani* in der lateralen Muskulatur beidseitig je ein ein Fenster, so daß ein Teil der vorderen Schwimmblasenkammer, nur von Haut überdeckt, in engem Kontakt mit dem Außenmedium Wasser steht. Die Wirbel 3 bis 5 sind miteinander verwachsen. Die Transversalfortsätze der Wirbel 4 und 5 bilden zusammen eine der Schwimmblase aufliegende Platte. Der anteriore Teil des Transversalfortsatzes des 4. Wirbels formt an seinem cranialen Ende einen Wulst, ähnlich wie bei *Pimelodus*. Ein Trommelmuskelapparat wurde bei *Pimelodella* jedoch nicht gefunden. Die herzförmige Schwimmblase erstreckt sich vom 2. bis zum 6. Wirbel und ist bei einem 123 mm großen Exemplar 8,5 mm lang. Sie wird von einem unvollständigen Diaphragma in eine anteriore und eine posteriore Kammer unterteilt. Das Diaphragma besitzt rechts und links je eine Öffnung, durch welche die beiden Kammern kommunizieren (Abb. 17). Die posteriore Kammer ist mindestens doppelt so lang wie die anteriore und wird durch ein vertikales Längsseptum vollständig zweigeteilt. Weitere Transversalsepten wurden, im Gegensatz zu *Pimelodus*, nicht gefunden. Der Ductus pneumaticus entspringt an der Schnittstelle des Längsseptums mit dem Diaphragma.

Lauterzeugung und Schreckreaktion

In Tabelle 3 sind diejenigen Welsfamilien aufgelistet, die auf den Besitz von Schreckstoffzellen und Schreckreaktion bzw. ihre Fähigkeit zur Lauterzeugung untersucht worden sind. Ferner zeigt diese Übersicht das Vorkommen sowie die Anzahl von Gattungen und Species nach Nelson (1994) und Teugels (1996). Der Reihenfolge der Familien liegt ein Cladogramm von de Pinna (1998) zugrunde, wobei die „niedrigen" Taxa zuerst genannt sind. Während 20 der 23 dargestellten Taxa Schreckstoffzellen besitzen, ist die Schreckreaktion nur bei 5 Welsfamilien durch Videoaufnahmen dokumentiert und bei 4 weiteren beobachtet worden. Stridulationsmechanismen treten bei 14, Trommelmechanismen bei 8 Familien auf. Beide Lauterzeugungsmechanismen gemeinsam kommen bei 7 der „höheren" Taxa vor.

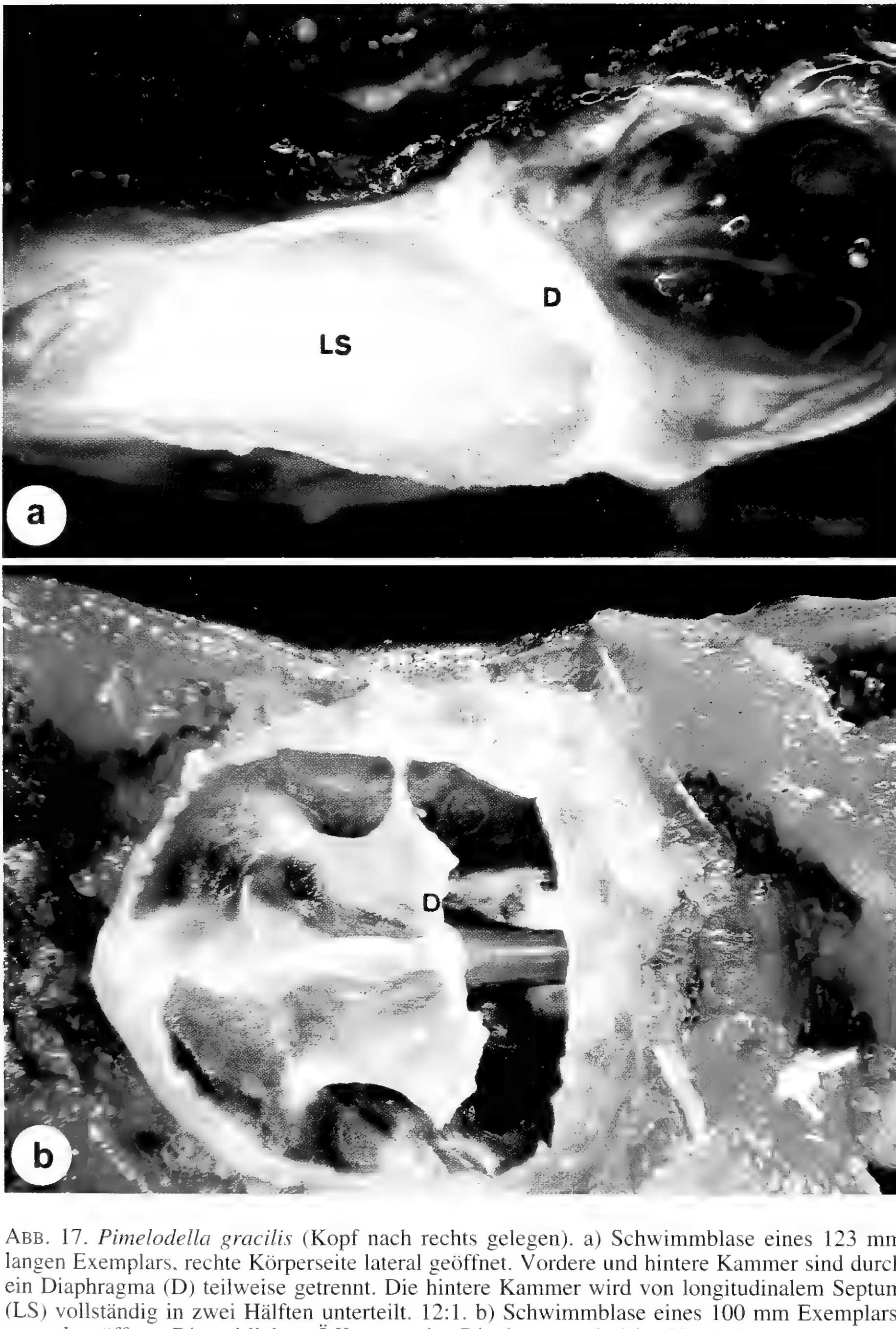


ABB. 17. *Pimelodella gracilis* (Kopf nach rechts gelegen). a) Schwimmblase eines 123 mm langen Exemplars, rechte Körperseite lateral geöffnet. Vordere und hintere Kammer sind durch ein Diaphragma (D) teilweise getrennt. Die hintere Kammer wird von longitudinalem Septum (LS) vollständig in zwei Hälften unterteilt. 12:1. b) Schwimmblase eines 100 mm Exemplars, ventral geöffnet. Die seitlichen Öffnungen im Diaphragma sind im Vergleich zu *Pimelodus pictus* großlumiger, weitere transversale Septen fehlen. 8:1.

TABELLE 3

Vorkommen, Anzahl der Gattungen (G.) und Species (Spec.) nach Nelson (1994) und Teugels (1996) sowie das Auftreten von Schreckstoffzellen (SZ), Schreckreaktion (SR), Stridulation (ST) und Trommelmechanismen (TM) bei verschiedenen Familien und Unterfamilien der Welse. Reihenfolge der Familien nach einem Cladogramm in de Pinna 1998, p. 289; Verwandtschaftsgruppen mit ● markiert. * : Unterfamilie der Pimelodidae = Rhamdiinae in Teugels 1996. **: Familie bei de Pinna 1998 nicht aufgelistet.
Abkürzungen: Ab = Abduktion; Ad = Adduktion; AF = Afrika; AS = Asien; D = Rückenflosse; E = Europa; MA = Mittelamerika; MAR = marin; NA = Nordamerika; PA = Pazifik; SA = Südamerika; SW = Süßwasser; TS = tropisch-subtropisch; V = Videoaufnahmen von SR vorhanden; + = vorhanden; (+) = SR gesehen; + ? = vorhanden, Mechanismus nicht beschrieben; ? = fraglich; -- = nicht vorhanden.

Familie	Vorkommen	G./ Spec. Nelson 1994	G. / Spec. Teugels 1996	SZ	SR	ST	TM
● Cetopsidae	SW / SA	4 / 12	4 / 14	+			
● Loricariidae	SW / SA, MA	80 / > 550	88 / 651	--	--	Ab	
Callichthyidae	SW / SA, MA	7 / 130	7 / 144	+	V	Ab	
Trichomycteridae	SW / MA, SA	36 / 155	40 / 154	+			
Amphiliidae	SW / AF	7 / 47	9 / 60	+			
Sisoridae	SW / AS	20 / 85	20 / 98	+		D	
● Aspredinidae	SW / SA	10 / 32	10 / 32	--	--	Ab+Ad	
● Heptapterinae*	SW / SA	-	18 / 220			Ab	
● Ictaluridae	SW / NA	7 / 45	7 / 45	+	(+)	Ab/Ab+Ad	
● Doradidae	SW / SA	35 / 90	37 / 94	+		Ab+Ad	+
Auchenipteridae	SW / SA	21 / 60	20 / 61	+		+	+
Mochokidae	SW / AF	10 / 167	11 / 177	+	(+)	Ab+Ad	+
Ariidae	MAR (SW) / TS	14 / 120	14 / 148	+		Ab	+
● Siluridae	SW / E, AS	12 / 100	9 / 60	+	V		
Malapteruridae	SW / AF	1 / 2	1 / 3	+			+
Chacidae	SW / AS	1 / 3	1 / 3	+			
Plotosidae	MAR, SW / AS, PA	9 / 32	9 / 32	+	V	?	
Clariidae	SW / AF, AS	13 / 100	15 / 92	+	(+)	?	
● Pangasiidae	SW / AS	2 / 21	2 / 21	+	V	+	+
Schilbeidae	SW / AF, AS	18 / 45	13 / 51	+	V		
● Bagridae	SW / AF, AS	30 / 210	15 / 135	+		Ab+Ad	+
● Pimelodinae	SW / MA, SA	56 / 300	53 / 323	+	(+)	Ab	+
● Heteropneustidae**	SW / AS	1 / 2	1 / 2	+		+ ?	

DISKUSSION

LAUTERZEUGUNG:

Ariidae: Die Unterwasserlaute von *Arius felis* (Synonym *Galeichthys felis*) studierte Dobrin (1947). Diese Species erzeugt sowohl Laute mit dem Springfederapparat (Burkenroad, 1931) als auch Stridulationsgeräusche. Frisch gefangene *A. felis* brachten bei Bewegung der Brustflossen 30 - 50 ms lange Laute im Frequenzbereich 2 - 4 kHz hervor (Tavolga, 1960). *Arius seemani* produziert bei Abduktion der Brustflossen Stridulationslaute, deren Dauer und Frequenzanteile ebenfalls in diesem Bereich liegen. Die Lauterzeugung mittels Springfederapparat wurde von Tavolga

(1971b, 1976, 1977) eingehend untersucht. *Arius felis* erzeugt fast dauernd Trommellaute der Frequenz 100 Hz und benützt sie als primitives Echolot bis auf 10 cm Entfernung. Bemerkenswert ist die zu dieser tiefen Frequenz passende Hörschärfe. *Arius felis* hört im Bereich 50 - 1000 Hz, mit bester Hörschärfe bei 100 - 200 Hz (Popper & Tavolga, 1981). Diese Werte liegen weit unter denen von *Ameiurus nebulosus* (Ictaluridae) mit 100 - 4000 Hz bzw. 600 - 800 Hz (Poggendorf, 1952, Weiss *et al.*, 1969). In Feldstudien wurde gezeigt, daß *A. felis* besonders nachts Laute ausstößt, die dem Zusammenhalt der Gruppe dienen sollen. In Laborversuchen waren die Laute in Gesellschaft kürzer als unter Isolation. Ungestört gaben die Welse leise, 20 - 40 ms kurze Grunzer von sich; bei Störung dagegen wurden laute, 100 - 150 ms lange Geräusche mit einer Grundfrequenz von 150 Hz registriert (Tavolga, 1960, 1976). Bei Langzeituntersuchungen an *A. felis* fand Breder (1968), daß die Welse von April bis Oktober mit einer Sommerpause im Juli/August Laute erzeugten, hauptsächlich von 17 - 23 Uhr bei einer Wassertemperatur von 23 - 31°C. Die Trommelaktivität von *A. seemani* zeigte im Labor einen anderen Tag-Nacht-Rhythmus. Sie begann vor der Lichtperiode und war in den Morgenstunden am höchsten; nachts wurden kaum Laute registriert. Eine Funktion der Laute für den Zusammenhalt der Gruppe oder für die Orientierung im Dunkeln ist daher unwahrscheinlich. Bei Fischarten außerhalb der Welse wurden ebenfalls Dämmerungslaute (morgens und abends) beschrieben, deren biologische Bedeutung jedoch unbekannt ist (Winn, 1964; Zelick *et al.*, 1999).

Im Gegensatz zu den Untersuchungen an *A. felis* (Tavolga 1960) unterbrach *A. seemani* seine Trommelmuskelaktivität bei Störungen kurz, und die Lautdauer (ca. 200 ms) blieb vor und nach Störungen nahezu unverändert. Die Grundfrequenz der Laute lag mit 140 - 200 Hz im Bereich der von *A. felis* bekannten Kontraktionsfrequenz des Trommelmuskels (Fusionsgrenze < 400 Hz). Die anatomischen Übereinstimmungen zwischen beiden Species deuten darauf hin, daß auch bei *A. seemani* die Grundfrequenz der Laute der Kontraktionsfrequenz des Protractors entspricht. Die Pausen zwischen den Lauten eines isolierten *A. seemani* schwankten in Ruhe und bei Störung. *Arius seemani* besitzt einen Springfederapparat wie *A. felis* (Tavolga 1962). Einen solchen Apparat führen auch die Auchenipteridae, Bagridae, Doradidae, Malapteruridae, Mochokidae und Pangasiidae (Müller, 1842; Bridge & Haddon, 1893; Chranilov, 1929; Tavolga, 1962). Sörensen (1884) sowie Bridge & Haddon (1894) wiesen bereits darauf hin, daß der Springfederapparat der Doradidae der Lauterzeugung dient, wie von Kastberger (1977, 1978) bestätigt. Entsprechendes gilt für die Mochokidae (Abu-Gideiri & Nasr, 1973). Der Springfederapparat und der direkte Trommelmechanismus (bei Pimelodidae) haben sich möglicherweise bei verschiedenen Welsfamilien unabhängig voneinander entwickelt (Alexander, 1965). Der Funktionsmechanismus des Springfederapparats läßt sich folgendermaßen beschreiben: Durch Kontraktion des Trommelmuskels (Protractors) werden der „Müller'sche Ramus" (Tavolga, 1962) und der Transversalfortsatz des 4. Wirbels (Knochenplatte) craniad bzw. dorsad bewegt. Weil der Müller'sche Ramus über Bindegewebe mit der Tunica externa der vorderen Schwimmblasenkammer verwachsen ist, wird die Schwimmblase bei seiner Bewegung mitgezogen. Entspannt sich der Protractor,

schnellen Knochenplatte und Müller'scher Ramus wieder zurück. Die vordere Schwimmblasenkammer wird komprimiert und ihr Gasinhalt in die hintere Kammer gepreßt. Die Schwimmblase ist durch Transversalsepten unterteilt. Das an den Septenrändern und dem Diaphragma vorbeiströmende Gas versetzt diese in Schwingung. Die Schwimmblasenwand wird zum Vibrieren angeregt und ihre Schwingung durch die trommelnden Knochenelemente verstärkt (vergleichbar einem Schlagzeug). Die Schwimmblase dient als Resonanzkörper (Trommel). Schwingungsgeneratoren sind der Trommelmuskel und die knöchernen Elemente. Die Synchronisation der beiden Trommelmuskeln, rechts und links am jeweiligen Müller'schen Ramus, wird zurückgeführt auf die polyaxonale und multiple Versorgung ihrer Fasern durch den zweiten Spinalnerven (Schneider, 1967).

Aspredinidae: Die Stridulationslaute von *Bunocephalus* spec. wurden von Winn (1964) analysiert und von Pfeiffer & Eisenberg (1965) an einigen Species gehört. Die Kontraktionsdauer der Muskelpotentiale von *Bunocephalus* spec. entspricht mit 100 ms der Lautlänge (Gainer, 1967). Die Lautdauer von *Dysichthys coracoideus* ist mit 80 ms nur wenig kürzer. Wie *Bunocephalus* spec. striduliert *D. coracoideus* bei Abduktion und Adduktion.

Auchenipteridae: Sie besitzen neben der Brustflossenstridulation auch einen Springfederapparat (Müller 1842). Die Trommellaute von *Trachycorystes* spec. haben eine Grundfrequenz von 120 Hz und können einige Sekunden andauern (Kastberger, 1978). Weitere Daten zu Schwimmblasen- und Stridulationslauten finden sich bei Kaatz (1999).

Bagridae: *Leiocassis micropogon* erzeugt „knurrende", *L. siamensis* und *L. poecilopterus* produzieren „krächzende" Laute. *L. brashnikowi* gibt „einzelne Töne" von sich, und beim Paarungsspiel von *Mystus vittatus* entstehen „zwitschernde" Laute (Riehl & Baensch, 1983; Franke, 1985; Sterba, 1990), wobei der Mechanismus der Lauterzeugung nicht genannt wird. *Mystus vittatus* und *M. gulio* stridulieren bei Abduktion und Adduktion der Brustflossen. Mit den „Quietschlauten" von *Hemibagrus nemurus* gibt es eine weitere, nämlich pneumatische Weise der Lautentstehung. Agassiz (1852) hörte bei einem Wels Geräusche, die anscheinend durch Luftausstossen aus der Schwimmblase hervorgerufen wurden. Bei *Synodontis schall* ist ein „Atemgeräusch" vernehmbar, das vermutlich mit der Schwimmblase zusammenhängt (Dufossé 1874). Sörensen (1895) beschrieb ein katzenähnliches Fauchen („not unlike the hissing of a cat") beim Zitterwels *Malapterurus* und führte dies auf die zwischen hinterer und vorderer Schwimmblasenkammer durch einen dünnen Gang streichende Luft zurück. Kaatz (1999) beobachtete Lauterzeugung durch Luftausstoßen bei 8 Welsfamilien.

Callichthyidae: *Callichthys callichthys* läßt bei der Brutpflege „grunzende" Laute hören (Riehl & Baensch, 1983). *Hoplosternum thoracatum* erzeugt bei Geschlechtsreife im Wasser Stridulationslaute (Mayr 1987). Für *Dianema urostriata* wurden Stridulationslaute nur bei Abduktion nachgewiesen, wie von *H. thoracatum* bekannt. Bei *Corydoras paleatus* stridulieren beide Geschlechter beim Fang, die Männchen auch bei Balz und Paarung (Pruzsinsky & Ladich, 1998).

Clariidae / Heteropneustidae: Stridulationsgeräusche wurden für *Heteropneustes fossilis* beschrieben. Die Laute entstehen zum einen durch Bewegung der Brustflossen, zum anderen durch Reiben der Pharyngealzähne am Mundboden. Es wird vermutet, daß die Laute der Warnung und Abwehr von Angreifern sowie während der Fortpflanzungsperiode der Schwarmbildung dienen (Agrawal & Sharma 1965). Diese Species, früher zu den Clariidae gezählt, wird heute den Heteropneustidae zugeordnet (Burgess, 1989; Teugels, 1996). Über die Lauterzeugung der Clariidae gibt es kaum Zeugnisse: Tennent (1859; zitiert in Sörensen, 1895, p. 115f.) berichtet über Aussagen von Fischern, nach denen ein „Magoora" genannter Fisch in einem See nahe Colombo bei Störung im Wasser „Grunzlaute" hervorbringt. Nach Day (1881) handelt es sich dabei um einen Wels der Gattung *Clarias*, wahrscheinlich um *Clarias magur* („Mah-gur" oder „Magurah", Day, 1958), einem Synonym von *Clarias batrachus* (Eschmeyer, 1998). Der Laut soll durch Schwimmblasenluft entstehen, die über den Ductus pneumaticus entweicht (Sörensen, 1895). Es könnte sich aber auch um Stridulationslaute handeln, da viele Clariidae kräftige Brustflossenstacheln besitzen, deren Struktur derjenigen stridulierender Species ähnelt (Nawar 1954).

Doradidae: *Acanthodoras spinosissimus* „grunzt" (Innes 1956), „knurrt" (Sterba 1956), „krächzt" und gibt einen lang anhaltenden Quarrlaut von sich, der aus einer Folge von Einzellauten besteht (Villwock, 1960). *Amblydoras hancocki* erzeugt knurrende Töne, und *Platydoras costatus* stößt beim Fangen „quakende" Laute aus (Sterba 1990). Die Lauterzeugung in Abhängigkeit von der Bewegung der Brustflossen wurde erstmals von Pfeiffer & Eisenberg (1965) experimentell untersucht, durch gleichzeitige Film- und Tonbandaufnahmen von *Agamyxis albomaculatus*, *Amblydoras hancocki* und *Platydoras costatus*. Die Laute entstehen bei Abduktion und Adduktion, wobei die Abduktionslaute länger sind als die Adduktionslaute. Die an *Agamyxis flavopictus* erhobenen Befunde bezüglich Laut- und Pausenlängen entsprechen den Ergebnissen von Pfeiffer & Eisenberg (1965). Dagegen fand Ladich (1997), daß sich Ab- und Adduktionslaute bei *Agamyxis pectinifrons* bzw. *Platydoras costatus* in der Länge nicht unterscheiden. Die Dauer der Stridulationslaute liegt bei den beiden Species *A. flavopictus* und *A. pectinifrons* mit ca. 100 ms im gleichen Bereich. *A. flavopictus* wird im Handel oft als *A. pectinifrons* bezeichnet (Franke 1985). *Hassar orestis* kann ebenfalls stridulieren und ist durch seine abgespreizten Flossenstacheln sogar vor Piranhas geschützt (Markl, 1968). Neben der Brustflossenstridulation besitzen die Doradidae einen indirekten Trommelmechanismus, den "Springfederapparat" (Müller, 1842; Sörensen, 1884, 1895; Bridge & Haddon, 1894; Dorn, 1976; Kastberger, 1977, 1978). Die biologische Bedeutung der durch die Brustflossenstridulation erzeugten Laute sehen Pfeiffer & Eisenberg (1965) im „Schutz oder der Verteidigung", in der Warnung eines potentiellen Beutegreifers vor einem nur schwer zu verschlingenden, gefährlichen Happen. Die Gefährlichkeit ist gegeben durch die Sperrmechanismen der Stacheln von Brustflossen und Rückenflosse (Brousseau, 1976), in Verbindung mit ihrer großen mechanischen Festigkeit (Schaefer, 1984) und möglichen Giftigkeit (Birkhead, 1972), die sogar für den Menschen tödlich sein kann (Nelson, 1994).

Ictaluridae: Den Bau des Schultergürtels von *Ictalurus nebulosus* beschreibt Brousseau (1976). *I. nebulosus* striduliert bei Abduktion und Adduktion, wodurch die Anzahl der aggressiven Auseinandersetzungen zwischen dem Revierinhaber und einem Eindringling herabgesetzt wird (Rigley & Muir, 1979). Dagegen striduliert *Ictalurus punctatus* nur bei Abduktion, meistens mit der rechten Brustflosse (Fine *et al.*, 1996, 1997). Daß *Ictalurus nebulosus* nach Lundberg (1992) zur Gattung *Ameiurus* gehört, könnte den Unterschied im Stridulationsmechanismus erklären. Jedoch sind nach Eschmeyer (1998) beide Gattungsnamen für diese Species gültig. Die Sperrmechanismen des Rückenflossenstachels und der Brustflossenstacheln schützen *I. melas* weitgehend davor, von Reihern und Rothalstauchern gefressen zu werden, die ihre Beute nicht zerteilen, nicht aber vor Seeadlern, die sie zerlegen. Die beiden kleineren Vogelarten fressen überwiegend Barsche (Forbes, 1989).

Loricariidae: *Plecostomus* spec. striduliert und besitzt ein ähnliches Brustflossenskelett wie die Doradidae und Mochokidae (Pfeiffer & Eisenberg, 1965). *Peckoltia pulcher* und *Glyptoperichthys gibbiceps* stridulieren nur bei Abduktion. Bei *Pterygoplichthys* spec. beträgt die Lautdauer 250 ms, die Grundfrequenz 500 Hz, die Pausendauer 400 - 600 ms. Große Exemplare zeigen eine kürzere Laut- und Pausendauer und ein höher liegendes Frequenzspektrum als kleine (Schachner, 1977). Flossenstacheln und Schultergürtel von *Pterygoplichthys* spec. sind von enormer mechanischer Stabilität (Schaefer, 1984).

Mochokidae: *Synodontis* spec. ist bereits vor 170 Jahren als erster durch Stridulation Laute erzeugender Wels in die Literatur eingegangen (Geoffroy Saint-Hilaire, 1829). Aus Daget *et al.* (1986) geht hervor, daß es sich hierbei um *Synodontis schall* (Bloch & Schneider, 1801) handelt. Diese Species striduliert bei Abduktion und Adduktion der Brustflosse (Müller, 1857, Dufossé, 1874) wie *S. nigrita* und *S. nigriventris* (Pfeiffer & Eisenberg, 1965), *S. ocellifer* und *S. schoutedeni*. Die Befunde an *S. ocellifer* und *S. schoutedeni* entsprechen in jeder Beziehung (Lautmechanismus, Laut- und Pausendauer, Struktur der Sonagramme und Frequenzschwerpunkte) den vor 35 Jahre vom Zweit-Autor erhobenen (Pfeiffer & Eisenberg, 1965). Alle geprüften Mochokidae stridulieren schneller als die Doradidae, weshalb die Dauer ihrer Laute und Intervalle kürzer ist. Ladich (1997) konnte keinen signifikanten Unterschied in den Lautlängen zwischen diesen beiden Familien finden, was für die Abduktionslaute knapp zutrifft ($p = 0.08$). Die Adduktionslaute der Doradidae waren länger als die der Mochokidae. Zur Klärung dieser Frage sollten weitere Species beider Familien untersucht werden. Die Mochokidae besitzen außer der Brustflossen-Stridulation auch einen Springfederapparat (Sörensen, 1884, 1895; Bridge & Haddon, 1893). *S. schall* striduliert und trommelt. Er soll Laute erzeugen bei Verfolgung, „Schmerz", aggressivem Verhalten, Laichverhalten und als Reaktion auf Berührungsreize (Abu-Gideiri & Nasr, 1973).

Pangasiidae: *Pangasius sutchi* erzeugt Stridulationsgeräusche (Kaatz, 1999).

Pimelodidae: Bau und Funktion des Stridulationsapparates und des Trommelmechanismus wurden von Schachner (1977) an *Pimelodus* spec. untersucht. Schachner & Schaller (1982) zeigen, daß es sich dabei um *Rhamdia sebae* handelt und beschreiben Defensivgeräusche (Stridulation), Drohlaute (Intervalle 60 - 70 ms) und

„Störungslaute“ (Trommellaute wie die Drohlaute, jedoch mit kürzeren Intervallen von nur 10 - 20 ms und höherer Frequenz). Die Stridulationsgeräusche dauern 40 - 85 ms, im Mittel 54 ms; ihr Energieschwerpunkt liegt bei 2 kHz (Schachner 1977). Die Stridulationsgeräusche von *Brachyrhamdia meesi* entstehen nur bei Abduktion der Brustflosse, wie diejenigen von *R. sebae*. Auch bei dem von Kratochvil *et al.* (1980) und Kratochvil & Völlenkle (1981) untersuchten *Pimelodus* spec. dienen die Stridulationslaute bei Rivalenkämpfen als Warnlaute, zur Revierverteidigung und bei interspecifischen Attacken. Stoß und Biß werden mit Stridulationsgeräuschen beantwortet. Akustische Drohsignale können Fluchtreaktionen auslösen. Die Trommellaute dienen der innerartlichen Verteidigung, die Stridulationslaute der Warnung. Den Feinbau der Trommelmuskeln beschreibt Dorn (1976). Die für die Lauterzeugung verantwortlichen Motoneuronen identifizierten Ladich & Fine (1994) an *Pimelodus blochi* und *P. pictus*. Drei Äste des N. occipitalis und die beiden ersten Spinalnerven versorgen das Trommelorgan, ein rostraler Ast des N. occipitalis und die beiden ersten Spinalnerven die Stridulationsmuskeln (Abduktor und Adduktor). *Pimelodus pictus* zeigte Drohverhalten gegenüber Artgenossen durch Spreizen seiner Flossen und Kiemendeckel, gleichzeitig Trommellaute erzeugend, wie von Schachner & Schaller (1982) für *Rhamdia sebae* geschildert. Auch die Strukturen des Trommelmechanismus von *P. pictus* entsprechen weitgehend der Beschreibung für *R. sebae*. In beiden Fällen handelt es sich um einen direkten Trommelmuskelapparat. Der anteriore Teil des transversalen Fortsatzes vom 4. Wirbel bildet einen Wulst, an dem der Trommelmuskel ventral entspringt. Bei beiden Species setzt der Trommelmuskel S-förmig an der ventralen Schwimmblasenwand an, wobei er bei *P. pictus* etwas weiter über den caudalen Rand der vorderen Schwimmblasenkammer hinwegzieht als bei *R. sebae*. Die Kammerung des posterioren Schwimmblasenteils ist verschieden: bei *R. sebae* treten zahlreiche Transversalsepten auf, bei *P. pictus* nur drei. Lautbildung und Funktion der Transversalsepten einschließlich des Diaphragmas der Schwimmblase wurden bereits von Sörensen (1884, 1895) beschrieben. Durch Kontraktion des Trommelmuskels wird die vordere Schwimmblasenkammer komprimiert und ihr Gasinhalt in die hintere Kammer gepreßt. Beim Entspannen des Muskels wird das Gas wieder zurückgesogen. An den Rändern der unvollständigen Transversalsepten vorbeistreichend versetzt es diese in Vibration und regt die gesamte Schwimmblase zum Schwingen an. Der kontraktierende Trommelmuskel erzeugt das Geräusch, das durch die Schwingungen von Septen und Schwimmblase verstärkt wird. Sörensen (1895) schnitt winzige Löcher in die Schwimmblasenwand, wodurch der Laut an Intensität verlor. Doch war der Laut sogar nach Entfernen der Schwimmblase noch schwach zu hören. Dagegen war nach Durchtrennung des paarigen Trommelmuskels kein Geräusch mehr wahrzunehmen. Bei *R. sebae* sind im posterioren Schwimmblasenabschnitt nur die Septen beweglich, die Schwimmblasenwand ist starr (Schachner & Schaller, 1982). Außer den Septen wird vor allem der vordere Schwimmblasenabschnitt zum Schwingen angeregt, so daß die Vibrationen beidseitig über die lateralen Fenster in der Muskulatur direkt an das umgebende Wasser abgegeben werden können. Bei der Präparation der Schwimmblase von *P. pictus* war auffallend, daß ihr posteriorer Teil stabiler ist als ihr anteriorer. Wurde die

Schwimmblase lateral eröffnet, fiel die vordere Kammer zusammen, während die hintere stabil blieb. Der posteriore Schwimmblasenteil wird durch die Transversalsepten und die festere Wand gestützt. Tavolga (1962) reizte Trommelmuskeln von *Bagre marinus* elektrisch: die zur Dauerkontraktion notwendige Frequenz beträgt 500 Hz. Die Fasern der Trommelmuskeln von *P. pictus* gehören zu den schnell zuckenden und sind dicht kapillarisiert. Ontogenetisch leiten sich die Trommelmuskeln von Myotom-Muskulatur ab, die in Richtung Peritoneum gewandert ist und sich diesem aufgelagert hat. Das Peritoneum ist an der Ansatzstelle des Trommelmuskels an der Schwimmblase mit deren Tunica externa verwachsen (Alexander, 1965). Der direkte Trommelmuskelapparat deutet darauf hin, daß *P. pictus* Trommellaute erzeugt. *Pimelodella gracilis* besitzt wie *Pimelodus pictus* beidseits je ein Fenster in der Muskulatur, Transversalfortsätze des 4. und 5. Wirbels und eine gut ausgebildete Schwimmblase. Ein Trommelmuskel konnte bei *P. gracilis* nicht gefunden werden. Da nur juvenile Weibchen untersucht wurden, ist nicht auszuschließen, daß der Trommelmuskel bei diesen Fischen entweder noch nicht entwickelt war oder nur bei Männchen existiert. Die folgenden Tatsachen sprechen gegen einen Trommelapparat bei *P. gracilis*: ein derart mächtiger Trommelmuskel, wie ihn *P. pictus* und *Arius seemani* haben, wird vermutlich bereits in einem frühen Entwicklungsstadium angelegt; die untersuchten juvenilen *P. pictus* besaßen bereits einen Trommelmechanismus. Ferner spricht die Form der Schwimmblase von *P. gracilis* gegen eine Funktion als Lautorgan. Schließlich fehlen der hinteren Schwimmblasenkammer Transversalsepten, die nach Sörensen (1895) für die Lauterzeugung notwendig sind. Die posteriore Kammer ist durch ein Longitudinalseptum zweigeteilt. Das Gas in der Schwimmblase hat nur die Möglichkeit, an den Diaphragma-Rändern entlang in eine dieser beiden hinteren Kammern zu gelangen. Zudem ist die vordere Kammer von *P. gracilis* die kleinere, im Gegensatz zu *P. pictus*. Es könnte also nur ein geringes Gasvolumen bewegt werden, um das Diaphragma und die Schwimmblasenwände zum Schwingen anzuregen. Die beiden lateralen Fenster in der Muskulatur und die knöchernen Elemente des 4. und 5. Wirbels sind für das Hören wichtig (Alexander, 1965). Diese Fenster verringern den Widerstand der Körperwand, so daß die Schwimmblase Schallschwingungen fast ungedämpft aufnehmen kann, um sie über die ihr craniad-dorsad aufliegenden Weberschen Knöchelchen an das Innenohr weiterzuleiten.

Plotosidae: Burgess (1989) zitiert Beschreibungen von *Plotosus lineatus*, in denen diese Species auch „bumblebee catfish" (Hummelwels) genannt wird. Demnach soll ein Summen hörbar sein, sobald man diese Welse aus dem Wasser fischt. Auch bei Störungen im Wasser wurden solche Geräusche vernommen. Da ein Schwimmblasenmechanismus bei dieser Species nicht beschrieben wurde, könnte es sich um Stridulationslaute handeln.

Siluridae: Stridulationsgeräusche wurden für diese Familie bisher nicht beschrieben. Bei Hawkins (1986) findet sich aber folgende Bemerkung: „Some catfish of the family Siluridae produce a squeak when the enlarged pectoral spines are moved." Da eine Quellenangabe fehlt, handelt es sich möglicherweise um eine Verwechslung mit anderen Welsfamilien.

Sisoridae: Im Gegensatz zu allen anderen Welsfamilien stridulieren die beiden bisher untersuchten Sisoridae nicht mit den Brustflossen, sondern mit der Rückenflosse, wie von Haddon (1881) an *Gagata gagata* entdeckt und von Mahajan (1963) an *Sisor rhabdophorus* bestätigt. Die Lauterzeugung geschieht bei Abduktion und Adduktion der Rückenflosse und dient vermutlich dazu, Beutegreifer vor der Gefährlichkeit oder Ungenießbarkeit des Fisches wegen seiner kräftigen Brustflossenstacheln und seines Rückenflossenstachels zu warnen.

Trommelmechanismen sind nach der Stridulation die häufigste Form der Lauterzeugung. Die Frage, ob die Schwimmblase für die Lauterzeugung notwendig ist, wird unterschiedlich beantwortet, obwohl es auch lauterzeugende Fische ohne Schwimmblase gibt. Während die Schwimmblase schon früh als hydrostatisches Organ erkannt wurde (Boyle, 1670, 1675; Ray, 1675), ist ihre große Bedeutung für Hörvermögen, Weberschen Apparat, Lauterzeugung und akustische Kommunikation erst seit dem 19. und 20. Jahrhundert bekannt: (1) *Hörvermögen* (anatomisch): Weber, 1820; Reissner, 1859; Bridge & Haddon, 1893; Chranilov, 1929 und Chardon, 1968; (physiologisch) von Frisch & Stetter, 1932; Poggendorf, 1952 und Weiss *et al.*, 1969; (Reviews) Harden Jones & Marshall, 1953; Alexander, 1964, 1965, 1966; Popper & Fay, 1973, 1993; Rogers *et al.*, 1988 und Schellart & Wubbels, 1998; (2) *Lauterzeugung* (anatomisch): Müller, 1857; Dufossé, 1874; Moreau, 1876; Sörensen, 1884, 1895 und Bridge & Haddon, 1889; (Reviews) Harden Jones & Marshall, 1953; Schneider, 1961, 1967 und Demski, *et al.*, 1973; (3) *akustische Kommunikation* (Reviews): Tavolga, 1960, 1971a, 1977, Fine, *et al.*, 1977; Myrberg, 1981; Hawkins & Myrberg, 1983; Michelsen, 1983; Urick, 1983 und Tyack, 1998.

Die Schwimmblase ist bei der Lauterzeugung durch Trommelmechanismen der Siluroidei beteiligt (Müller, 1857; Tavolga, 1962; Ladich, 1997). Durch ihre Gasfüllung fungiert sie als Impedanzwandler zwischen den Trommelmuskeln und dem Wasser und verstärkt so die erzeugten Schwingungen. Es wird diskutiert, ob dabei diejenigen Frequenzen am besten verstärkt werden, die ihrer Resonanzfrequenz entsprechen (Demski *et al.*, 1973). Kaatz (1995) fand bei mehreren Species der Auchenipteridae und Doradidae Korrelationen zwischen der Schwimmblasengröße und der Hauptfrequenz der erzeugten Laute. Bei Fischarten außerhalb der Siluroidei wurde festgestellt, daß größere Exemplare tiefere Laute hervorbringen. Dies wird auf veränderte Resonanzeigenschaften der Schwimmblase zurückgeführt (Demski *et al.*, 1973), da die Resonanzfrequenz mit zunehmendem Volumen der Schwimmblase sinkt (Urick, 1983). Es muß dabei berücksichtigt werden, daß die Schwimmblase von verschiedenen Geweben umgeben ist, die Schwingungsdämpfungen bewirken und ihre Resonanzeigenschaften beeinflussen. Bei Stridulationsgeräuschen ist die Beteiligung der Schwimmblase umstritten: in der Lautstärke besteht außerhalb des Wassers bei intakten Doradidae und Mochokidae einerseits und Exemplaren mit eröffneter Schwimmblase andererseits kein Unterschied (Pfeiffer & Eisenberg, 1965). Zur selben Ansicht kamen Fine *et al.* (1997) bei Untersuchungen an *Ictalurus punctatus*: hier spielt die Schwimmblase bezüglich Frequenzspektrum und Amplitude der Stridulationslaute zumindest keine Hauptrolle, während eher der Schultergürtel auf die

Frequenzverteilung Einfluß nimmt. Andererseits ergaben Untersuchungen an *Corydoras paleatus*, daß die Hauptfrequenz der Stridulationslaute mit zunehmender Körpermasse abnimmt (Pruzsinsky & Ladich 1998). Es wäre möglich, daß hier veränderte Resonanzeigenschaften der Schwimmblase eine Rolle spielen. Ob stridulierende Fische die Resonanzfrequenz ihrer Schwimmblase modulieren, wurde bisher nicht untersucht (Zelick *et al.*, 1999).

Lauterzeugung und Phylogenie

Wichtige Fragen zu den Welsen (Berg, 1958; Nelson, 1976; Burgess, 1989) sind ungelöst. Über die Phylogenie und das Natürliche System gibt es verschiedene, zum Teil konträre Meinungen (Eigenmann & Eigenmann, 1890; Regan, 1911, Greenwood *et al.,* 1966; Rosen & Greenwood, 1970; Roberts, 1973; Lauder & Liem, 1983; Fink & Fink, 1981, 1996; Schaefer, 1987). Die Klassifizierung in Familien sowie die Anzahl der Gattungen und Species hat sich laufend verändert (Tab. 3; Mo, 1991; Nelson, 1994; Teugels, 1996). Auch die Verbreitungsgeschichte der Welse ist unklar: diskutiert werden primäre Zentren in Südamerika und Südostasien, ein sekundäres Zentrum in Afrika (Gosline, 1975) oder Entstehung in Südamerika bzw. Südostasien (Novacek & Marshall, 1976; Briggs, 1979). Die Fossilgeschichte ist ebenfalls unbefriedigend; vermutlich war die interkontinentale Verbreitung schon vor dem Eozän abgeschlossen (Gosline, 1975). Innerhalb der Siluroidei gibt es so viel Parallel-Evolution, daß die phylogenetischen Zusammenhänge bei unserem gegenwärtigen Wissensstand unklar bleiben (Alexander, 1965; Teugels, 1996; de Pinna, 1998).

In ihrer Kommunikation zeigen die Welse ein vielfältiges Bild. Sie verfügen über mindestens 6 verschiedene Möglichkeiten der Lauterzeugung (Tab. 3): (1) Stridulation durch Abduktion der Brustflossen (Ariidae, Callichthyidae, Ictaluridae, Loricariidae, Pimelodidae), (2) Stridulation durch Abduktion *und* Adduktion der Brustflossen (Aspredinidae, Bagridae, Doradidae, Ictaluridae, Mochokidae), (3) Stridulation mit der Rückenflosse (Sisoridae), (4) pneumatische Mechanismen durch Luftausstoßen über die Kiemenspalten (*Hemibagrus nemurus*), (5) direkter Trommelmechanismus (*Pimelodus pictus*) und (6) indirekter Trommelmechanismus oder Springfederapparat (*Arius seemani*). Innerhalb der Familien und Gattungen können verschiedene Mechanismen auftreten oder fehlen. Bei den Loricariidae gibt es neben stridulierenden Species nichtstridulierende, sogar innerhalb derselben Unterfamilie (Ancistrinae; Schaefer 1987). Doch sind die Verwandtschaftsverhältnisse innerhalb der Loricariidae ungeklärt. Nach Untersuchungen mit Hilfe der rRNA-Sequenzierung sind alle Unterfamilien außer den Loricariinae paraphyletisch (Montoya-Burgos *et al.* 1998).

Bei den Bagridae stridulieren *Mystus gulio* und *M. vittatus*, während *H. nemurus* mit Hilfe der Kiemenspalten quietscht. Auch der Stridulationsmechanismus kann in derselben Familie wechseln (Ictaluridae: *Ameiurus*, *Ictalurus*). Innerhalb derselben Species treten stridulierende und nichtstridulierende Individuen auf, wobei der Anteil der stridulierenden Exemplare unterschiedlich ist. Die einzelnen Parameter der Geräusche wie Häufigkeit, Wiederholungsrate, Laut- und Intervalldauer, Laut-

stärke oder Frequenzanteile variieren bei Familien, Arten, Angehörigen derselben Species und sogar bei ein und demselben Individuum. Die an einer Species erhobenen Befunde lassen sich weder für eine Familie noch für eine Gattung verallgemeinern.

Die weite Verbreitung der Lauterzeugung durch Stridulation der Brustflossen sowie die weitgehend ähnliche strukturelle Ausbildung des Stridulationsapparates deuten daraufhin, daß dieser Mechanismus bei manchen Familien sekundär teilweise oder ganz verlorengegangen ist. Die Stridulationsmechanismen Abduktion und Adduktion der Brustflossen sind sowohl gemeinsam als auch allein (nur Abduktion) in allen größeren Verwandtschaftsgruppen zu finden (de Pinna, 1998; Tab. 3). Entsprechende Untersuchungen der Basisgruppen der Welse (Diplomystidae, Cetopsidae u.a.) liegen bisher nicht vor. Stridulationslaute treten außer bei Störungen auch beim Fortpflanzungsverhalten mancher Species auf (Mayr, 1987; Pruzsinsky & Ladich, 1998; Kaatz & Lobel, 1999). Es gibt Hinweise, daß der Lauterzeugungsapparat bei diesen Species sekundär abgewandelt wurde (Kaatz & Stewart, 1997).

Die Schwimmblasenmechanismen sind unterschiedlich gestaltet, doch nicht familiencharakteristisch, wie Ladich (1997) meint. Bei den Pimelodidae besitzt *Pimelodus pictus* einen Trommelmechanismus, *Pimelodella gracilis* nicht. Es könnte sich dabei um einen Unterschied zwischen Unterfamilien handeln, da *Pimelodus* zu den Pimelodinae, *Pimelodella* aber zu den Rhamdiinae (Teugels, 1996) gestellt wird. Die letztgenannte Gruppe wird von de Pinna (1998) als Heptapterinae bezeichnet, deren Phylogenie ungeklärt ist. Doch treten auch innerhalb derselben Unterfamilie (Pimelodinae, *Calophysus*-Gruppe) Species mit und ohne Schwimmblasenmuskeln auf (Stewart, 1986; de Pinna, 1998). Weder bei den Basisgruppen Diplomystidae, Cetopsidae noch bei der nächsthöheren, 12 Familien umfassenden, Gruppe (Loricariidae-Callichthyidae-Aspredinidae-Trichomycteridae u.a.; de Pinna, 1998) ist bisher ein Trommelmuskelapparat gefunden worden.

Lauterzeugung und Schreckreaktion

Die Schreckreaktion auf Schreckstoff aus der Haut von Artgenossen wurde von Karl von Frisch (1938) an der Elritze *Phoxinus phoxinus* (L.) (Cyprinidae) entdeckt und später auch an fünf anderen Species der Cyprinidae nachgewiesen. Hautextrakt von 20 weiteren Species einheimischer Cyprinidae und zwei Species der Cobitidae löste bei Elritzenschwärmen ebenfalls eine Schreckreaktion aus. Dagegen waren die Häute von allen Fischen, die nicht zu den Cyprinidae und Cobitidae gehören, darunter der nordamerikanische Zwergwels *Ameiurus nebulosus*, unwirksam. Der einzige Versuch mit diesem Wels endete negativ (von Frisch, 1941a,b). Zwei Schüler von Karl von Frisch setzten die von ihm begonnenen Versuche über die Verbreitung der Schreckreaktion fort: F. Schutz (1956) und W. Pfeiffer (1960 bis heute). Nach Schutz (1956) ist die Schreckreaktion unter den Cyprinidae allgemein verbreitet, selbst wenn es sich nicht um ausgesprochene Schwarmbildner handelt. „Die gleiche Reaktion findet sich auch bei kleineren, friedlich lebenden und schwarmbildenden Characidae.“ Auch alle vier Versuchsgruppen von *Ameiurus nebulosus* zeigten in acht Versuchen immer ein positives Ergebnis, das Schutz (1956)

jedoch als unspezifische Reaktion „von mehr ausweichendem als schreckhaftem Charakter“ betrachtete: „Trotz der Höhe der Konzentration der arteigenen Hautextrakte waren alle Reaktionen immer nur kurz und ohne nachhaltige Wirkung.“ Schutz (1956) war der Auffassung, daß eine Schreckreaktion bei den Zwergwelsen bemerkenswert wäre, weil die jüngeren Fische in Schulen zusammenhalten. Auch die kleinen Panzerwelse *Corydoras paleatus* (Callichthyidae) schwammen immer in einer Gruppe und zeigten auf ihren Hautextrakt „leicht schreckhaftes Verhalten.“ Ihre Reaktionsweise erzeugte bei Schutz (1956) jedoch den Eindruck, „daß es sich wie beim Zwergwels um eine unspezifische Reaktion handelt“.

Pfeiffer (1960) zeigte in fünf Versuchen an zwei Schwärmen des indischen Glaswelses *Kryptopterus bicirrhis* (Siluridae) erstmals, daß auch Siluroidei eine Schreckreaktion besitzen, die derjenigen der Cypriniformes und Characiformes gleichzusetzen ist. Dieses Ergebnis hat sich später an dieser und anderen Species der Welse bestätigt (Pfeiffer, 1963a; Pfeiffer *et al.*, 1986; Heyd & Pfeiffer, in Vorbereitung) und beweist, daß die Schreckreaktion bei den Ostariophysen (*sensu* Sagemehl 1885) allgemein verbreitet ist. Die Entdeckung der Schreckreaktion bei den Gonorynchiformes (Pfeiffer 1967) fügt sich in das System von Rosen & Greenwood (1970) ein, wonach die Ostariophysen *sensu* Sagemehl (1885) als Otophysi mit den Anotophysi (*alias* Gonorynchiformes) als Ostariophysi zusammengefaßt werden. Alle analogen Alarm-Pheromon-Systeme von nichtostariophysen Fischen (Cottidae, Gobiidae, Percidae) unterscheiden sich tiefgreifend von der Schreckreaktion der Ostariophysi (Smith, 1992). Nur die Ostariophysi (*sensu* Rosen & Greenwood, 1970) besitzen in ihrer Epidermis Schreckstoffzellen (Pfeiffer, 1960; Pfeiffer *et al.*, 1971), denen der Schreckstoff entstammt (Pfeiffer, 1960, 1963a, 1967; Smith, 1973, 1976a,b).

Ob die Schreckstoffzellen noch weitere Funktionen haben, wie von Pfeiffer (1967, 1970) für solitäre, nachtaktive Welse vermutet, ist nicht entschieden. Um die besondere Situation der Siluroidei, was ihre Schreckreaktion anbetrifft, zu verstehen, werfen wir zunächst einen Blick auf die anderen, wesentlich intensiver untersuchten Ostariophysi:

(1) Innerhalb der Cypriniformes wurde die Schreckreaktion bei allen mehr als 53 bisher geprüften Species aus fünf Familien gefunden, mit alleiniger Ausnahme des blinden Höhlenfisches *Caecobarbus geertsi*. Sie existiert bei allen tagaktiven Cyprinidae, auch bei bodenlebenden Species, sowie bei den Catostomidae, Cobitidae, Gyrinocheilidae und Homalopteridae. Auch die beiden räuberisch lebenden Cyprinidae *Leuciscus cephalus* und *Ptychocheilus oregonense* haben zumindest als Jungfische eine Schreckreaktion (Pfeiffer 1977).

(2) Innerhalb der Characiformes dagegen wurde die Schreckreaktion nur bei 2/3 der mehr als 50 geprüften Species gefunden. Es gibt hier Familien bzw. Unterfamilien, für welche die Schreckreaktion bisher nicht nachgewiesen werden konnte, nämlich die Chilodontidae, Lebiasinidae, Mylinae und Serrasalminae. Während das Fehlen der Schreckreaktion bei den räuberischen Piranhas verständlich ist, gilt dies nicht für die ihnen nahverwandten pflanzenfressenden und friedlichen Mylinae, es sei denn, man hält die Mylinae für Abkömmlinge der Serrasalminae. Beide, Serrasalm-

inae und Mylinae, besitzen Schreckstoffzellen und Schreckstoff, doch fehlt ihnen im ZNS die Fähigkeit, auf den Schreckstoff zu reagieren. Entsprechendes gilt für den blinden Höhlensalmler *Anoptichthys jordani* (Pfeiffer, 1967, 1977).

(3) Allen untersuchten Gymnotoidei fehlen Schreckstoffzellen und Schreckreaktion (Pfeiffer, 1963a, 1967).

(4) Bei *allen* 7 histologisch geprüften Gattungen der Anotophysi aus 4 Familien wurden Schreckstoffzellen gefunden. Für die beiden im Verhaltensexperiment getesteten Gattungen wurde die Schreckreaktion nachgewiesen. Von besonderer Bedeutung ist die wechselseitige Wirksamkeit des Schreckstoffs zwischen Otophysi und Anotophysi (Pfeiffer, 1967).

Von den ca. 33 Familien der Siluroidei wurden bisher 22 bezüglich ihrer Schreckstoffzellen untersucht. Bei 20 Welsfamilien wurden sie gefunden (Tab. 3), nur die Aspredinidae und Loricariidae führen keine (Pfeiffer, 1963c, 1977). Den Aspredinidae fehlen darüber hinaus sogar die Mauthner-Axone und damit der „Mauthner-Reflex", mit dem jede Schreckreaktion beginnt (Göhner & Pfeiffer, 1996, Pfeiffer *et al.*, 1986). Im Gegensatz zu den intensiv untersuchten Cypriniformes und Characiformes wurden bisher nur verhältnismäßig wenige Species und Familien der Siluroidei bezüglich ihrer Schreckreaktion geprüft (Pfeiffer, 1977), aus verständlichen Gründen, wie die Ergebnisse von Karl von Frisch (1938, 1941a, b) und Schutz (1956) zeigen. Die Schreckreaktion wurde bei Angehörigen der Clariidae, Ictaluridae, Mochokidae und Pimelodidae gesehen. Mit Sicherheit nachgewiesen, videotechnisch aufgezeichnet und analysiert wurde sie für *Kryptopterus bicirrhis* (Siluridae), *Pangasius sutchi* (Pangasiidae), *Eutropiellus vanderweyeri* (Schilbeidae), *Corydoras paleatus* (Callichthyidae) und *Plotosus lineatus* (Plotosidae) (Pfeiffer, 1960, 1963a, 1977; Pfeiffer *et al.*, 1986, Heyd & Pfeiffer, in Vorbereitung).

Die Mehrzahl der Species und Familien der Welse sind abgeflachte Bodenfische mit hohem spezifischen Gewicht und unterständigem Maul, nachtaktiv und kleinäugig, mit Barteln als Trägern von Tast- und Geschmacksorganen und einem hervorragenden Hörvermögen. Sie sind meist solitär und wehrhaft durch kräftige Stacheln der Rückenflosse und der Brustflossen, die mit Sperrmechanismen ausgestattet und als Stridulationsapparate prädestiniert sind. Die meisten Welse ernähren sich von kleinen Invertebraten, einige sind Räuber, andere Algen- und Detritusfresser. Ihre nächtliche Aktivität und ihr Bodenleben teilen sie mit den Gymnotoidei, mit denen die Aspredinidae und Loricariidae auch das Fehlen von Schreckstoffzellen sowie mehrere andere Welsfamilien den Besitz von Elektrorezeptoren („small pit organs") gemeinsam haben. Ihre Lebensweise als solitäre nachtaktive Bodenfische unterscheidet die meisten Siluroidei und alle Gymnotoidei deutlich von den gewöhnlich gesellig lebenden, tagaktiven, größtenteils pelagischen Cypriniformes, Characiformes und Anotophysi. Die Welsarten mit der am deutlichsten ausgeprägten Schreckreaktion sind ebenfalls tagaktive Schwarmfische oder zumindest als Jungfische in Gruppen lebend. Sie erinnern durch ihr Aussehen und ihre Lebensweise an die große Mehrzahl der Cypriniformes und Characiformes. *Corydoras* ist zwar bodenlebend, doch tagaktiv und besonders in der Jugend in Gruppen lebend. *Synodontis* hat wie die Bodenfische ein unterständiges Maul, ist jedoch pelagisch und nimmt Nah-

rung von der Wasseroberfläche rückenschwimmend auf. *S. nigriventris* ist dementsprechend sogar invers pigmentiert, wie sein Name verrät. Auch junge Ictaluridae und Pimelodidae bilden Schulen. Die pelagischen *Eutropiellus*, *Kryptopterus*, *Pangasius* und *Plotosus* sind tagaktiv und zumindest als Jungtiere ausgesprochene Schwarmfische. Weil die Schreckreaktion ihre Aufgabe nur bei schwarmbildenden, tagaktiven Fischen voll erfüllen kann, ist sie bei solitären, nachtaktiven Species nicht zu erwarten. Der Schreckstoff dient nicht dem Sender, sondern allein den Empfängern. Selektioniert wird nicht das Individuum, sondern die Gruppe. Nur wenn alle Schwarmmitglieder gemeinsamer Abstammung wären, kann man von „kin"-Selektion sprechen; meist handelt es sich um Gruppen-Selektion. Solitäre, mit kräftigen Stacheln bewehrte Fische schützen sich selbst. Im Gegensatz zu den nachtaktiven, meist kleinäugigen Welsen sind die tagaktiven Species großäugig, was zu der Tatsache paßt, daß die Schreckreaktion visuell übertragen wird.

Lauterzeugung durch Stridulation ist von mindestens 14 Welsfamilien bekannt, Trommelmechanismen von 8 Familien (Tab. 3). In 7 Familien treten beide Mechanismen auf. Der elektrische Zitterwels besitzt einen Trommelapparat (Müller, 1842), ohne zu stridulieren. Er wehrt sich mit seinen starken Entladungen, wie sonst nur Zitterrochen und Zitteraal. Von den trommelnden *und* stridulierenden Familien besitzen die Mochokidae und Pimelodidae die Schreckreaktion, von den *nur* stridulierenden die Ictaluridae und Callichthyidae. Während den stridulierenden Aspredinidae und Loricariidae Schreckstoffzellen *und* Schreckreaktion fehlen, sind von den pelagischen Welsen mit besonders gut ausgebildeter Schreckreaktion nur vereinzelt Stridulationsmechanismen bekannt. Schreckreaktion und Lauterzeugung schließen einander zwar nicht aus, aber es ist auffallend, daß sie entsprechend der Lebensweise der Fische verbreitet sind. Viele nachtaktive, bodenlebende, wehrhafte, solitäre Welse können durch Stridulation Abwehrlaute erzeugen. Die tagaktiven, schwarmbildenden Welse zeigen eine Schreckreaktion. Doch ist es gegenwärtig wenig ratsam, einen nur an wenigen Species erhobenen Befund für eine ganze Familie zu verallgemeinern. Aufgrund unvollständiger Untersuchung ist unser bisheriges Bild lückenhaft. Deshalb sollten Schlüsse über den Zusammenhang zwischen dem Auftreten von Lauterzeugungsmechanismen einerseits und dem Vorkommen der Schreckreaktion andererseits nur mit Vorsicht gezogen werden.

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Molecular and morphological evidence for the presence of a new Buthid taxon (Scorpiones: Buthidae) on the Island of Cyprus

Benjamin GANTENBEIN*[1], Christian KROPF[2], Carlo Rodolfo LARGIADÈR[1] & Adolf SCHOLL[1]
[1] Division of Population Biology, Institute of Zoology, University of Berne, Baltzerstrasse 3, CH-3012, Berne, Switzerland.
e-mail: Gantenbein@zoo.unibe.ch
[2] Natural History Museum Berne, Department of Invertebrates, Bernastrasse 15, CH-3005 Berne, Switzerland.
e-mail: christian.kropf@nmbe.unibe.ch

Molecular and morphological evidence for the presence of a new Buthid taxon (Scorpiones: Buthidae) on the Island of Cyprus. - Allozyme data (16 loci) from *Mesobuthus gibbosus* populations in the eastern Mediterranean region show that the Cyprus population is highly distinct, although morphological differentiation is rather weak. This provides evidence for a 'hidden' taxon on Cyprus. This island population is described as a new species.

Key-words: Allozymes - Scorpiones - *Mesobuthus* – new species - Cyprus.

INTRODUCTION

Comparison of molecular data from insular and continental populations of a species or of closely related species may provide new insights into the process of speciation with respect to time (Estoup *et al.*, 1996; Baldwin & Sanderson, 1998; Beerli *et al.*, 1996; Gillespie *et al.*, 1998; Hollocher, 1998; Widmer *et al.*, 1998). Island populations are of particular interest for the analysis of colonisation processes (Vachon & Abe, 1988) or for studying founder effect speciation (Templeton, 1980, 1981; Carson & Templeton, 1984; Grant, 1998). *Mesobuthus gibbosus* (Brullé, 1832) (Scorpiones: Buthidae) is widely distributed in the eastern Mediterranean region (Werner, 1928, 1937, 1938; Vachon, 1947a, 1947b, 1948, 1966; Tolunay, 1959; Gruber, 1963, 1966; Kinzelbach, 1975, 1982, 1984, 1985; Vachon & Kinzelbach, 1987; Kritscher, 1993; Crucitti, 1993). Its geographical range includes the mainland (south Balkan, Peloponnesus, Anatolia) and eastern Mediterranean islands (e. g. Cyclades, Sporades, Crete

*to whom correspondence should be addressed

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and Cyprus). The geographic variation within scorpion species was traditionally examined by using morphological characters like patterns of trichobothria (='trichobothriotaxy') (Vachon, 1974, 1975, 1976; Fet, 1986; Fet & Rechkin, 1989) or variation in the number of pectinal teeth (Kinzelbach, 1975; Michalis & Kattoulas, 1981; Michalis & Dolkeras, 1989). The taxonomic status of different populations of *M. gibbosus* has remained unclear: Kinzelbach (1975) distinguished two subspecies, *M. g. gibbosus* (Brullé, 1832) (south of the Balkan Peninsula, Northern Sporades, Cyclades) and *M. g. anatolicus* (Schenkel, 1947) (Crete, Anatolia, Cyprus). Kritscher (1993) doubted the validity of *M. g. anatolicus* and rejected it.

The widely accepted theory of the salinity crisis (Hsü, 1972; Hsü *et al.*, 1977) states that the Mediterranean sea dried out 5.6 Myrs ago and, consequently, the colonisation of islands via landbridges was possible during a period of 100'000 yrs. Since the refilling of the basin (5.2 Myrs ago) the populations became geographically isolated. Since then, a considerable degree of differentiation between mainland and island populations is expected to have taken place. Alternatively, other genetic population structures than expected are likely if scorpions were introduced by man. Because of several introductions of euscorpiids (Stockwell 1992) caused by man (e. g. Benton, 1991; Goyffon, 1992; Toscano-Gadea, 1998), island populations might not be as isolated as expected.

To clarify the status of some island populations and of the Cyprus population in particular, we carried out a comparative genetic analysis at 16 allozyme loci. Populations from the Peloponnesus, from the south of the Balkans, from Crete, Rhodes, Anatolia and from Cyprus were included. We describe here new morphological characters, which distinguish *Mesobuthus* from Cyprus from the other populations of *Mesobuthus gibbosus* examined.

MATERIAL & METHODS

Specimens analysed. Samples were collected at two sites on the Peloponnesus, GR (Vigla [Arta]; Mathia [Messinia]), two sites on Crete, GR (Vai; Zakros [both in Lassithi]), two sites on Rhodes, GR (Petaloudes; Kolympia), two sites in central Anatolia, TR (Avanos; Hacibectas [both Cappadocia]), one site in southern Anatolia, TR (Selale [Pamphylia]) and two sites on northern Cyprus (Tepebasi; Kantara [both Turkish part]). The scorpions were transported alive to the laboratory, killed by deep-freezing and stored at -80°C prior to electrophoresis. For the morphological examination, the specimens were later transferred into 75% ethanol. *Androctonus mauretanicus* (Pocock, 1902) from Agadir (MA) and *Androctonus crassicauda* (Olivier, 1807) from Urfa (TR) were used as outgroup species for phylogenetic analyses. The sampling sites are shown in Fig. 1.

Allozyme analysis. Horizontal starch gel electrophoresis of allozymes was carried out according to the protocols described in Gantenbein *et al.* (1998) and Murphy *et al.* (1996). We scored 16 loci on three buffer systems: N-(3-Aminopropyl)-morpholine-citrate (AC, pH 6.2, modified from Clayton & Tretiak, 1972), Tris-citrate (TC, pH 7.3, Ayala *et al.*, 1972) and Tris-borate-EDTA (TBE, pH 9.3, modified from Ayala *et*

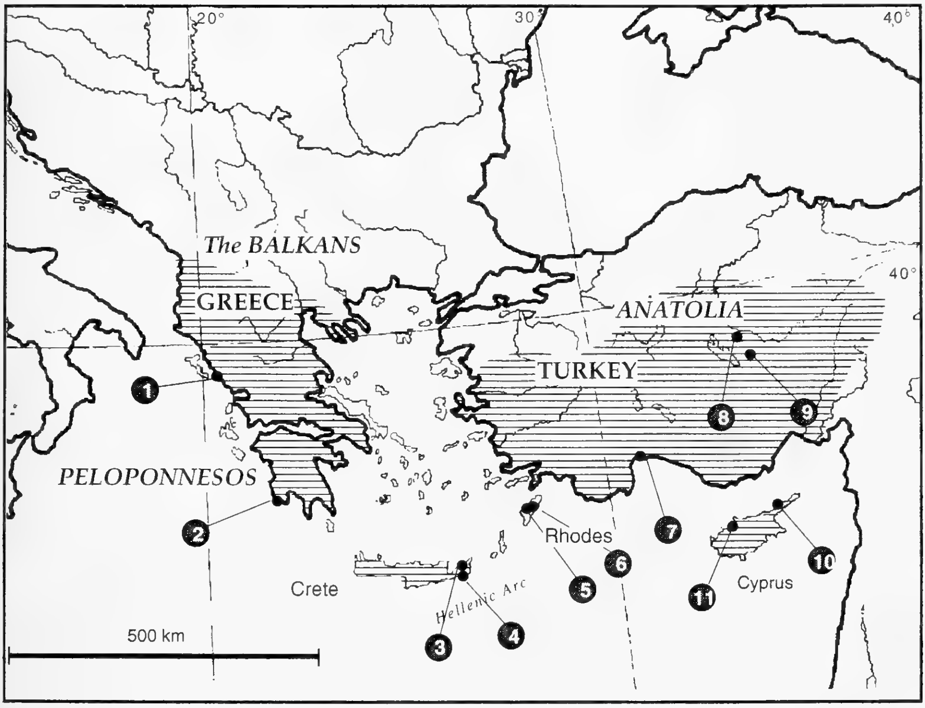


FIG. 1

Sampling sites of the analysed *Mesobuthus* populations: 1: Vigla, GR, 2: Mathia, Gr, 3: Vai, GR, 4: Zakros, GR, 5: Kolympia, GR, 6: Petaloudes, GR, 7: Selale, TR (3 sites), 8: Hacibectas, TR, 9: Avanos, TR, 10: Kantara, TR, 11: Tepebasi, TR.

al., 1972). The loci scored were: ALPDH (Alanopine dehydrogenase; EC 1.5.1.17), ARK (arginine kinase; EC 2.7.3.3), AAT-1 and AAT-2 (aspartate aminotransferase; EC 2.6.1.1), DDH (dihydrolipoamide oxidase; EC 1.8.1.4), PGI (GPI) (glucose-6-phosphate isomerase; EC 5.3.1.9), GTDH (glutamate dehydrogenase; EC 1.4.1.2), IDH-1 and IDH-2 (isocitrate dehydrogenase; EC 1.1.1.42), MDH-1 and MDH-2 (malate dehydrogenase; EC 1.1.1.37), MPI (mannose-6-phophate isomerase; EC 5.3.1.8), PGM (phosphoglucomutase; EC 5.4.2.2), 6-PGD (6-phosphogluconate dehydrogenase; EC 1.1.1.44), PK (pyruvate kinase; EC 2.7.1.40), and SOD (superoxide dismutase; EC 1.15.1.1). We refer to the observed electromorphs as alleles which are identified by their electrophoretic mobility relative to the most common mobility in the *Euscorpius flavicaudis* (de Geer, 1778) population from Lauris, France (assigned mobility=100) as described in Gantenbein *et al.* (1998). To assess the genetic variability within each population, the mean number of alleles per locus, the percentage of polymorphic loci and the mean heterozygosity were calculated by the direct count method and by Nei's (1978) unbiased estimate. Nei's genetic distance (1972) was calculated from pairwise

comparisons of populations using the program GENDIST from the PHYLIP 3.5 package (Felsenstein, 1995). Nei's distance is expected to rise linearly with time since the complete separation of gene pools, if sufficiently large numbers of loci are measured (Felsenstein 1984; Nei 1987). Using Nei's pairwise distances as an input matrix, an additive tree was created by the neighbour-joining algorithm (NJ) (Saitou & Nei, 1987). NJ is assumed to be a good heuristic approach for estimating the minimum evolution tree (Page & Holmes, 1998) and allows for different rates among lineages in contrast to the UPGMA clustering algorithm. Alternatively, an unrooted maximum likelihood tree was calculated using the computer program CONTML. It estimates phylogenies by the restricted maximum likelihood (REML) method, based on the Brownian motion model (Cavalli-Sforza & Edwards, 1967). The REML algorithm was formerly described in Felsenstein (1973, 1981) and uses less parameters than the full ML analysis and is, therefore, assumed to be more consistent. Additionally, the program calculates branch lengths and rough confidence intervals for the branches. Bootstrap values were obtained based on 1000 pseudo-replicates of allele frequencies using the SEQBOOT routine in PHYLIP.

RESULTS

Genetic variability. In general, the observed genetic variability was rather low within the *Mesobuthus* samples. The mean observed heterozygosity was 0.07 ± 0.05, one to six out of 16 loci were polymorphic at the 0.95 criterion. The mean number of alleles ranged from 1.0 to 1.5 per locus. All analysed populations were fixed at many loci (Table 1). However, this variation was not evenly distributed among *Mesobuthus* samples. At five loci, more than two electromorphs were detected, whereas all populations were fixed for the same allele at three loci (Idh-2, Mdh-1, Pk). The Cyprus samples were fixed for private alleles (alleles that were not found in any other population) or showed polymorphisms with private alleles at six loci (Aat-1, Aat-2, Alpdh, Ldh-2, Mdh-2, 6-Pgd) in addition to minor differences in allele frequencies at the locus Mpi (Table 1). On the other hand, if compared to the mainland populations, the island populations from Crete and Rhodes showed private alleles at one locus only (samples Zakros and Vai at Aat-1 and samples Kolympia and Petaloudes at 6-Pgd, respectively). The island samples and the mainland samples differed mainly in the allele frequencies.

The outgroup comparison with *A. mauretanicus* and *A. crassicauda*, respectively, revealed alleles at eight loci that were not found in *Mesobuthus*, whereas, with respect to allele frequencies, the two Androctonus species differed from each other only at two loci.

TABLE 1

Allele frequencies and sample sizes of eleven *Mesobuthus* populations. *Androctonus mauretanicus* (MA) and *A. crassicauda* (TR) were used as outgroup species. Alleles were labelled as described in the material & methods section. Measures of genetic variability for each population are given at the bottom of the table. Private alleles of the Cyprus samples and the heterozygosity

Genus/species						*M. gibbosus*					*M. cyprius*		*Androctonus*	
Region		**Greek mainland**		**Crete**		**Rhodes**		**S. Anatolia**	**C. Anatolia**		**Cyprus**		**Morocco**	**Turkey**
Site		Vigla	Mathia	Zakros	Vai	Kolymbia	Petaloudes	Selale	Avanos	Hacibectas	Tepebasi	Kantara	Aourir	Urfa
Sample size		(2)	(15)	(5)	(2)	(6)	(6)	(16)	(5)	(3)	(20)	(4)	(14)	(6)
Locus	Allele													
Aat-1	111													0.08
	104												1.00	0.75
	94													0.17
	82	1.00	1.00			1.00	1.00	1.00	1.00	1.00	0.30			
	80										**0.70**	**1.00**		
	75			1.00	1.00									
Aat-2	117										**0.35**	**0.63**		
	110												1.00	
	109											**0.13**		1.00
	106	1.00	0.97	1.00	1.00	1.00	1.00	0.91	1.00	1.00	0.65	0.24		
	100	0.03					0.09							
Alpdh	105	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00				
	100										**1.00**	**1.00**	1.00	1.00
Ark	102			1.00	1.00	0.67	0.17	1.00	1.00	1.00			1.00	1.00
	98	1.00	1.00			0.33	0.83				1.00	1.00		
Ddh	99							1.00	1.00	1.00	0.05		1.00	1.00
	98	1.00	1.00	1.00	1.00	1.00	1.00				0.95	1.00		
Gtdh	100			1.00	1.00	0.67	0.25	1.00	1.00	1.00			1.00	1.00
	96	1.00	1.00			0.33	0.75				1.00	1.00		
Idh-1	104						0.08						1.00	1.00
	98	1.00	1.00	1.00	1.00	1.00	0.92	0.81	0.90	1.00	0.97	1.00		
	96								0.10					
	93										**0.03**			
	89							0.19						
Idh-2	93	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Mdh-1	105												1.00	1.00
	104	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00		
Mdh-2	92										**1.00**	**1.00**		
	82													0.08
	72	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00			1.00	0.92
Mpi	160	0.25	1.00	0.50		1.00	1.00	0.97	0.90	1.00	0.62	1.00		
	154	0.25		0.50	1.00			0.03	0.10					
	152										**0.38**			
	150												0.11	0.75
	145													0.25
	142	0.50												
	135												0.57	
	130												0.25	
	110												0.18	
6-Pgd	112					0.08	0.08							
	111												1.00	1.00
	104	1.00	1.00	1.00	1.00	0.92	0.92	1.00	1.00	1.00	0.03			
	100											**0.12**		
	93										**0.94**	**0.88**		
	82										**0.03**			
Pgi (GPI)	95	0.25				0.42	0.58	0.06			0.08		0.04	0.67
	87	0.75	1.00	1.00	1.00	0.58	0.42	0.94	1.00	1.00	0.92	1.00	0.96	0.33
Pgm	88	1.00	1.00			1.00	1.00		1.00	1.00	1.00	1.00	1.00	1.00
	81			1.00	1.00			1.00						
Pk	100												1.00	1.00
	98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00		
Sod	110			1.00	1.00	0.67	0.25	1.00	1.00	1.00				
	109												1.00	1.00
	103	1.00	1.00			0.33	0.75				1.00	1.00		
Mean no. of alleles per locus		1.2 (0.1)	1.1 (0.1)	1.1 (0.0)	1.0 (0.1)	1.3 (0.1)	1.4 (0.1)	1.3 (0.1)	1.1 (0.1)	1.0 (0.0)	1.5 (0.2)	1.2 (0.1)	1.2 (0.1)	1.3 (0.2)
Percentage of polymorhphic loci		12.5	0.0	6.3	0.0	31.3	37.5	18.8	12.5	0.0	37.5	12.5	6.3	25
Heterozygosity (observed)		0.06 (0.0)	0.0 (0.0)	0.01 (0.0)	0.0 (0.0)	**0.17** (0.1)	**0.14** (0.1)	0.04 (0.0)	0.03 (0.0)	0.0 (0.0)	0.08 (0.0)	0.06 (0.0)	0.03 (0.0)	0.09 (0.1)
Heterozygosity (expected)		0.08 (0.1)	0.0 (0.0)	0.04 (0.0)	0.0 (0.0)	**0.13** (0.1)	**0.12** (0.1)	0.04 (0.0)	0.03 (0.0)	0.0 (0.0)	**0.11** (0.1)	0.05 (0.0)	0.04 (0.0)	0.09 (0.1)

TABLE 2

Calculated pairwise distance matrix (Nei's D 1972) for all 13 samples of *Mesobuthus*. In bold are the genetic distance values of pairwise comparisons that involved one of the two Cyprus samples.

Region	Greek mainland		Crete		Rhodes		Anatolia			Cyprus		Outgroup
Population	Vigla	Mathia	Zakros	Vai	Kolympia	Petaloudes	Selale	Avanos	Hacibectas	Tepebasi	Kantara	Aourir
Vigla												
Mathia	0.03											
Zakros	0.42	0.41										
Vai	0.44	0.47	0.02									
Kolympia	0.13	0.10	0.21	0.26								
Petaloudes	0.05	0.03	0.35	0.42	0.05							
Selale	0.45	0.39	0.16	0.21	0.19	0.33						
Avanos	0.34	0.29	0.23	0.28	0.11	0.24	0.07					
Hacibectas	0.34	0.29	0.23	0.29	0.10	0.23	0.07	0.00				
Tepebasi	**0.31**	**0.28**	**0.78**	**0.84**	**0.44**	**0.33**	**0.87**	**0.70**	**0.69**			
Kantara	**0.39**	**0.33**	**0.82**	**0.92**	**0.50**	**0.39**	**0.95**	**0.78**	**0.77**	0.03		
Aourir	1.40	1.37	1.13	1.15	1.09	1.32	0.95	0.80	0.81	1.32	1.35	
Urfa	1.49	1.55	1.26	1.28	1.11	1.30	1.04	0.88	0.90	1.44.	1.46	0.14

Genetic differentiation and phylogenetic analyses. The calculated Nei's distances from pairwise comparisons of populations within *Mesobuthus* ranged from 0.00 to 0.95 (Table 2). The distance values between the two outgroup species and *Mesobuthus* were at least 0.80 and ranged up to 1.55. If the two samples from Cyprus are compared with the other *Mesobuthus* samples, it is obvious that the Cyprus populations are considerably distinct from all others, i. e. Vigla, Mathia, Kolympia, Petaloudes, Zakros, Vai (all GR), Selale, Avanos, Hacibectas (all TR), by rather high distance values (0.31 - 0.95).

The topologies of the NJ tree and of the maximum likelihood (ML) tree (-ln likelihood 544.123; 4909 trees examined) are generally congruent and differ from each other only in the position of the Cretean clade (Figs 2-3). This clade clusters separately in the NJ tree (Fig. 2) and groups with the sample of Selale (south Anatolia) in the ML tree (Fig. 3). However, both approaches revealed four main clades within *Mesobuthus* (Figs 2-3). The first clade is composed of the samples from the mainland of Greece (Vigla and Mathia) and island Rhodes (Petaloudes and Kolympia) and is found at a relatively low distance value. The two samples from Crete are found in a second independent clade, and the populations from Anatolia as a third clade. However, the Cyprus clade remains clearly separated from all other clades by a rather high tree length in both trees, and is confirmed as an offshot from the mainland. The bootstrap analysis supports four nodes of the trees with very high values (>90%), these are observed for the clades grouping the Cyprus samples (Tepebasi and Kantara), the central Anatolian samples (Avanos and Hacibectas), the Crete samples (Zakros and Vai), and the *Androctonus* species, respectively. The node between the Peloponnesian clade and the Cyprus clade is well supported (60% and 77%, respectively). *Androctonus* is confirmed as outgroup by a bootstrap value of 99%. However, the other nodes are weakly supported. The weakest support is found for the clade that contains the Cretean and Anatolian samples. Noteworthy, the outgroup species *A. mauretanicus* and *A. crassicauda* are separated by about the same genetic distance that is found among the samples

of the Peloponnesus / Rhodes clade and the Anatolian clade, although the outgroup samples are treated as different species and are geographically separated by a large distance (approximatively 3000 km).

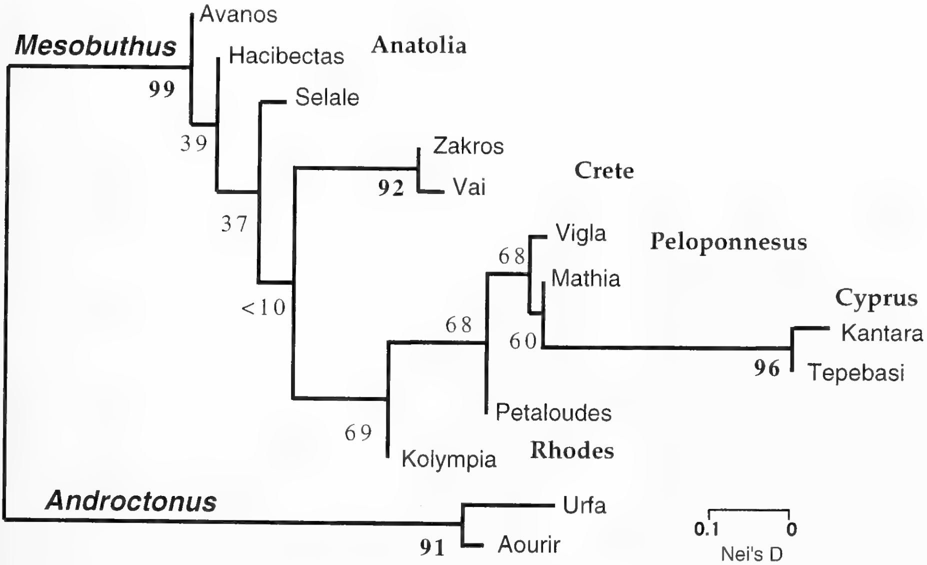


FIG. 2

NJ tree based on Nei's distance relating island and mainland populations of *Mesobuthus* inferred from 16 allozyme loci. *A. crassicauda* from Urfa (TR) and *A. mauretanicus* from Aourir (MA) were used as outgroups.

TAXONOMY

Mesobuthus cyprius Gantenbein & Kropf, sp. n. Figs 4-28; Tab. 1

Type material: Holotype: 1 male, Tepebasi, Northern Cyprus, 26. V. 1998, Natural History Museum Berne, Switzerland (NMBE). Paratypes (collected at the type locality): 1 male, 20. V. 1998, 1 female, 26. V. 1998, NMBE. 1 male, 20. V. 1998, 1 female, 26. V. 1998, Natural History Museum Basel, Switzerland; all specimens leg. A. Scholl (Berne, CH).

Other material examined: Morphology: *Mesobuthus cyprius* sp. n.: 6 males, 11 females from Tepebasi, 1 male, 1 female from Kantara, Cyprus. For a comparison, also specimens of *Mesobuthus gibbosus* from Rhodes, GR (31 specimens), Peloponnesus, GR (7), Crete, GR (20), Euboea, GR (1), Selale, TR (12) and central Anatolia, TR (3) were investigated.

Allozyme study: *Mesobuthus cyprius* sp. n., *Mesobuthus gibbosus*, *Androctonus mauretanicus*, *Androctonus crassicauda*: See Table 1.

Diagnosis: *Mesobuthus cyprius* sp. n. can be distinguished unambiguously only by the shape of the basal lobes of the hemispermatophores. These are slender and acutely pointed teeth in *Mesobuthus cyprius* sp. n. (Figs 8-9), while in all populations of *M. gibbosus* examined they form scales with more or less distinct blunt tips (Figs 29-

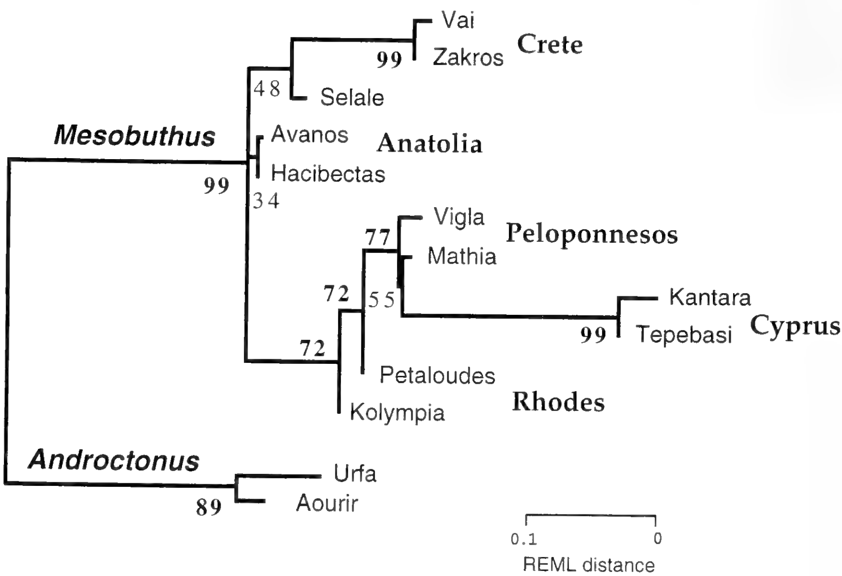


FIG. 3

Rooted maximum likelihood (ML) tree of island and mainland populations of *Mesobuthus*.

33; Vachon, 1948: fig. 1). Moreover, the hemispermatophore of the new species is considerably smaller than in *M. gibbosus*.

Description: *Measurements* (in mm): No apparent size dimorphism, although females longer, and males with a longer metasoma. Total length (measured dorsally from anterior margin of carapace to tip of stinger, with telson in horizontal position): Males 45-55, females 45-60. Carapace length (measured dorsally along midline): males 5.0-5.7, females 5.0-6.0. Carapace width (maximum distance between posterio-lateral edges): males 5.5-6.0, females 5.5-6.6. Metasoma length: males 28-37, females 27-35 (measured dorsally from anterior margin of first segment to tip of stinger).

Carapace (Figs 4, 5): trapezoid-shaped, colour pattern more or less distinct, especially lateral pigmented areas hardly visible in some specimens. Granulation: anterior median, central median and central lateral carinae distinct, granulae in remaining areas mostly weak. Anterior margin with transverse row of bristles.

Mesosoma (Figs 5, 6): Tergites I–VI with a pattern of pigmented longitudinal stripes, i.e. one median stripe and two pairs of lateral stripes (one paramedian, one ectal pair). These stripes partly broken, especially on tergite 6, colour varying from dark grey to medium brown (only alcohol preserved material examined, colour pattern more distinct in juveniles than in adults, in some adults hardly visible). Interspace between median and paramedian stripe less than 1-1,5 times as wide as paramedian stripe at posterior margin of tergites IV-VI. Tergite VII with more or less pronounced median

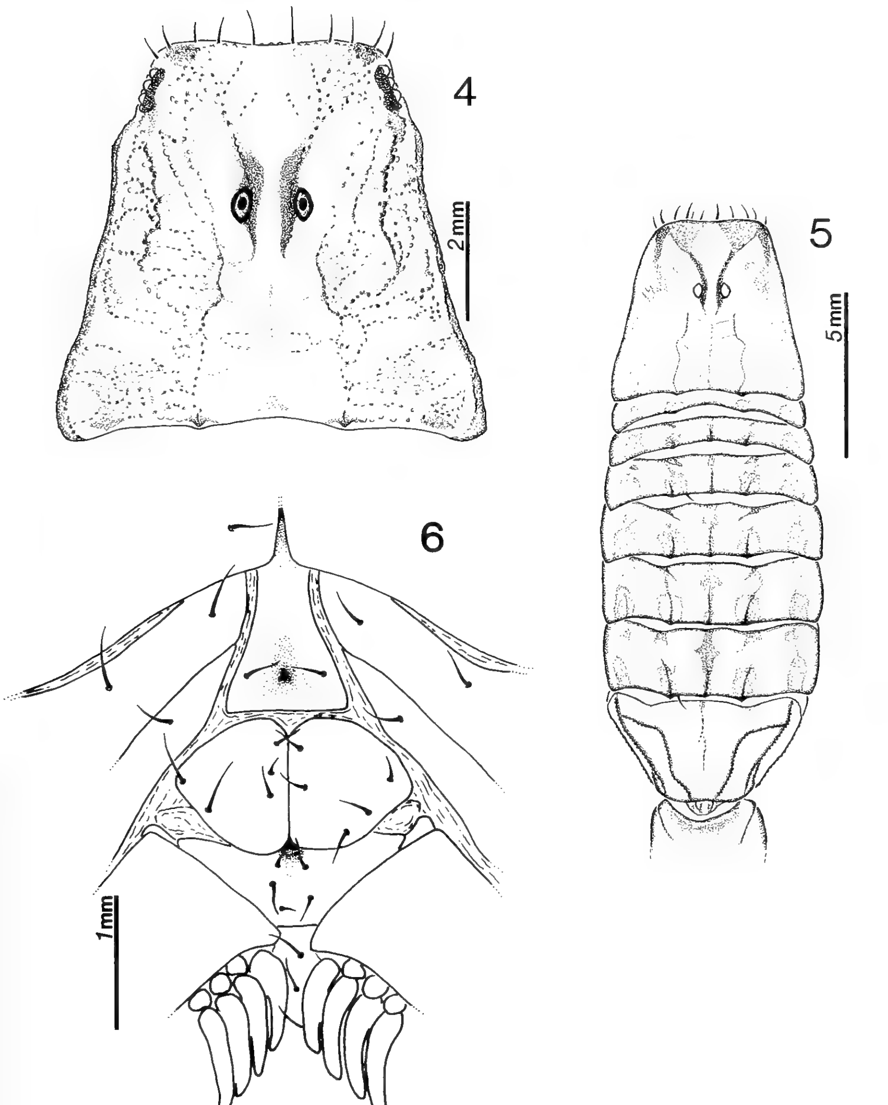


FIG. 4-6

Mesobuthus cyprius sp. n. – 4. Female carapace, dorsal view. – 5. Male carapace and mesosoma, dorsal view. – 6. Sternum and genital opercula, ventral view.

keel bearing granula. Tergites only sporadically with bristles or without. Sternites smooth, at least some of them with white guanin spots; these spots sometimes distributed all over the ventral and occasionally also the dorsal surface. Sternum subtriangular, with deep median depression flanked by a pair of bristles (Fig. 6). Genital opercula with a few scattered bristles (Fig. 6). Pectines with 20-23 (females) or 26-30 (males) teeth.

Hemispermatophore (Figs 7-9): Long, slender, of the flagelliform type. Four lobes at truncal flexure: internal lobe biggest, with a small distal hook, close to the external lobe, partly embracing it. Basal lobe developed as a slender and acutely pointed tooth.

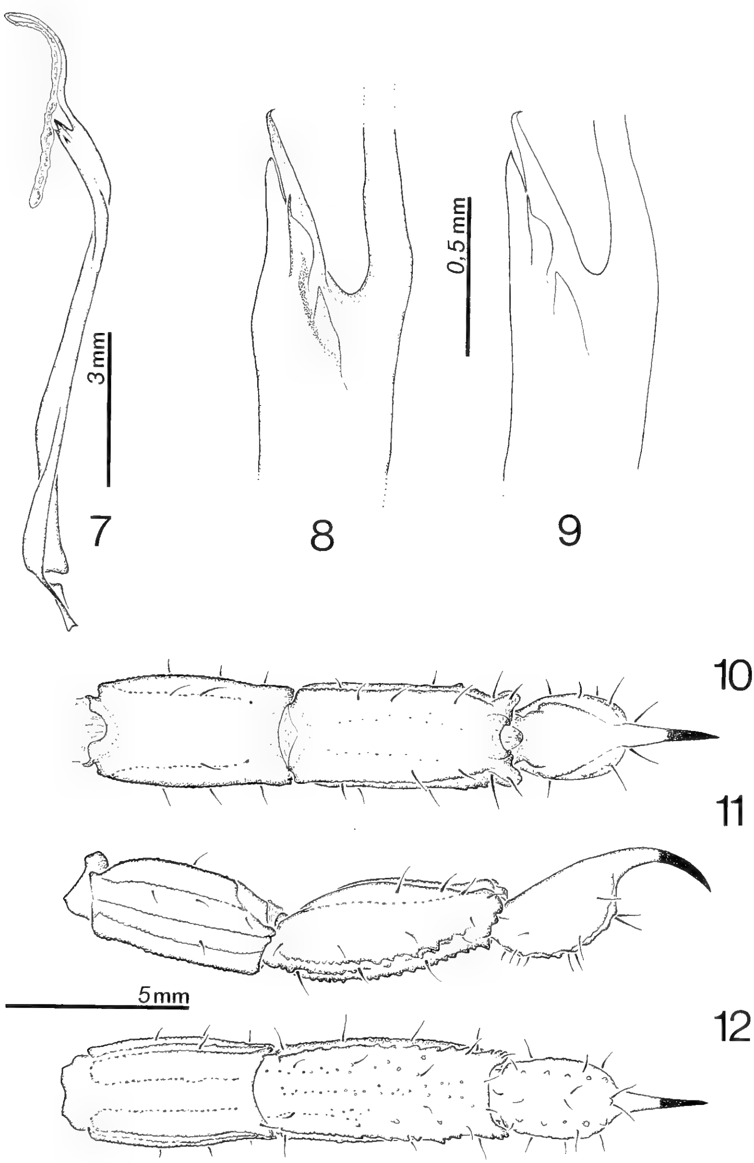
Metasoma (Figs 10-12): Segments I-IV with 10 longitudinal keels formed by rows of tubercles; one additional pair of keels mediodorsally being indistinct and hardly visible (not illustrated). Fourth segment 1.79 – 2.44 times longer than high in males, 1.54 – 1.58 times in females (length measured dorsally, height measured as distance between dorsal and ventral keel). Segment V granulate ventrally, with 3-4 blunt teeth laterally at distal edge. Telson with dark tip of stinger, granulate on ventral side, with several short bristles, one ventral pair of them rising from subaculeate tubercle.

Chelicera (Figs 13-14): Tibia (nomenclature following Hjelle 1990) with two large bristles dorsally near distal-prolateral edge, three shorter translucent hairs (several more of them on movable finger) and a brush of fine hairs prolaterally. Fixed finger with two ventral and four dorsal teeth; medial and basal dorsal tooth fused to form a bicusp. Movable finger with five dorsal teeth, the two basal ones being the smallest; ventrally with three teeth, i.e. one distal and two medial ones.

Pedipalp (Figs 15-23): Trichobothrial pattern constant, corresponding to type A of Vachon (1974). Femur a little shorter than patella, with 11 trichobothria, d2 (nomenclature of trichobothria following Sissom, 1990) short and translucent (Fig. 17). Patella with two distinct tooth-like tubercles ventro-proximally and with 13 trichobothria, d2 short and translucent (Figs 18-19). Chela slender, males with a weak lobe on movable finger (not illustrated). 15 trichobothria present; esb, Esb and Eb3 short and translucent (Figs 20-21). Teeth on inner side of fingers arranged in a characteristic pattern, interspersed with short, stiff bristles, i.e. groups of two retrolateral and one prolateral bristle and several of them at the tip (Figs 22-23).

Legs (Figs 24-28): increasing in length from leg 1 - 4. All legs with a pair of ventral pedal spurs distally on basitarsus. Proventral spur carrying a hair and a translucent tooth originating proximally on it (Fig. 28). Retroventral spur with a small tooth close to spur (Fig. 27). Legs 3 and 4 with a tibial spur distally (Fig. 26). Dorsal distitarsus with a conspicuous distal hair on an elevated base (Fig. 28). Apotele with three claws (Fig. 27).

R e m a r k s : *Mesobuthus cyprius* sp. n. differs from most populations of M. gibbosus by its pigmentation pattern on the mesosomal tergites, particularly by the width of the pale interspace between the median and the paramedian dark stripe which is less than 1-1.5 times the width of the latter at the posterior margin of tergites IV-VI. In most populations of *M. gibbosus*, the width of this interspace is at least more than 2 times the width of the paramedian stripe which may even be absent. However, this



FIGS 7-12

Mesobuthus cyprius sp. n. – 7. Left hemispermatophore, total view; surrounding tissue of paraxial organ removed, except in distal part of flagellum. – 8, 9. Lobes at truncal flexure. – 10. Metasoma segments 4, 5, and telson of male, dorsal view. – 11. Ditto, lateral view. – 12. Ditto, ventral view.

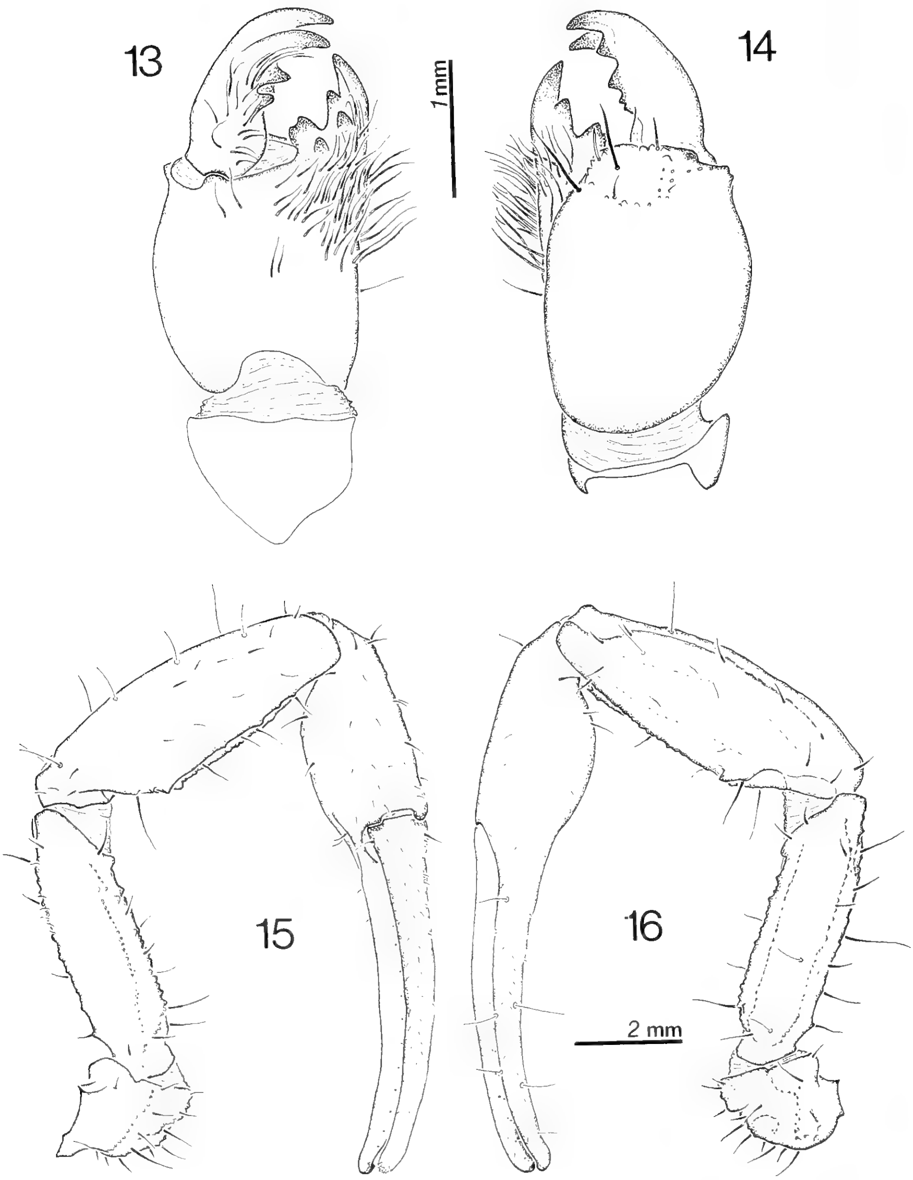
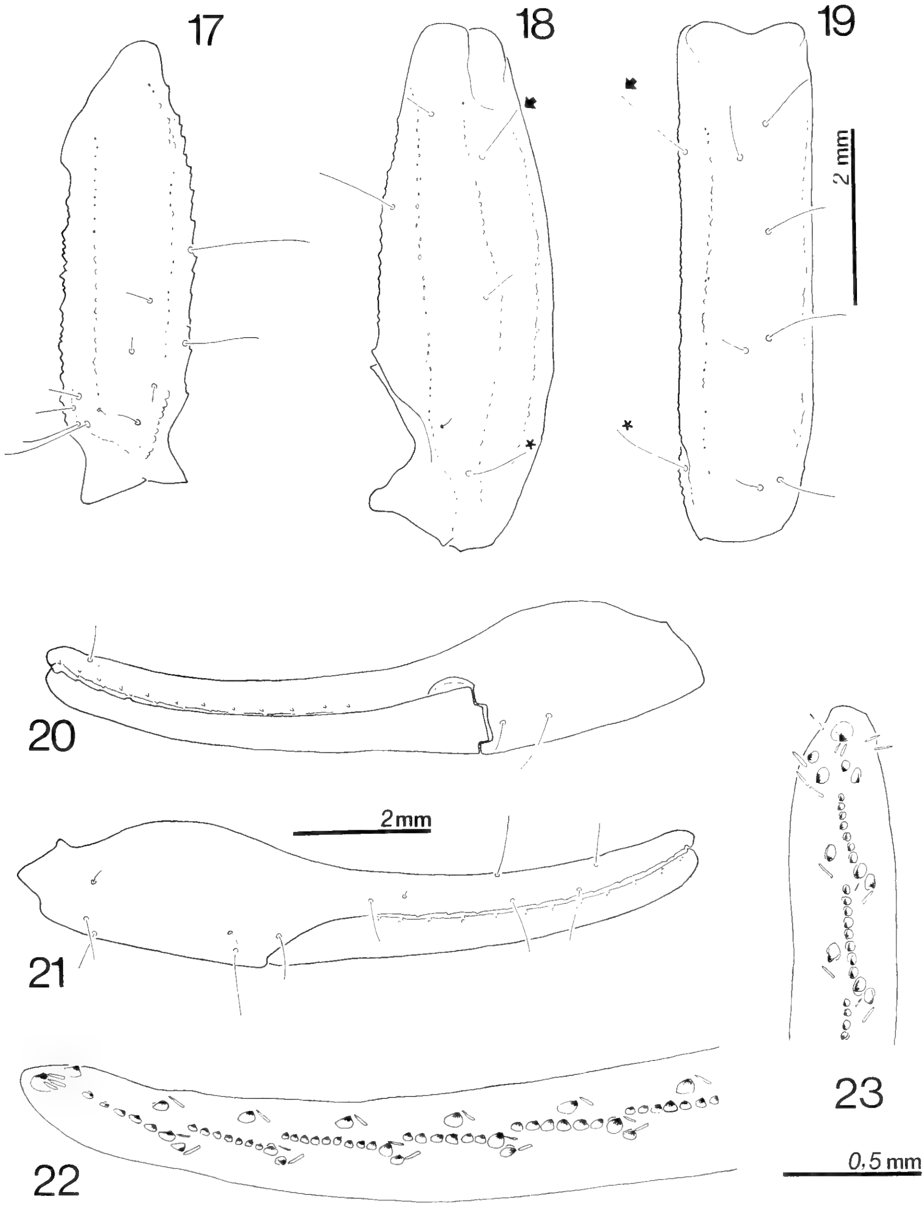


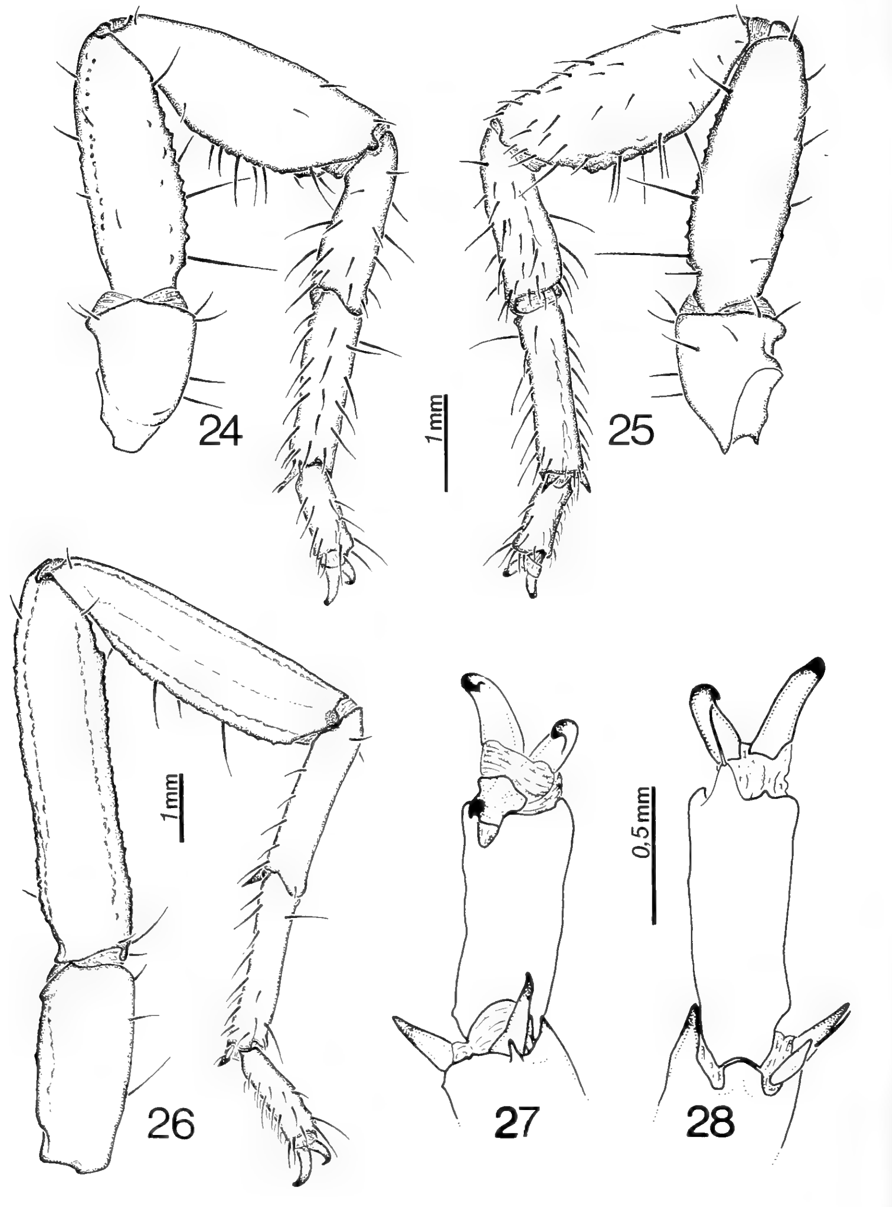
FIG. 13-16

Mesobuthus cyprius sp. n., male – 13. Right chelicera, ventral view; prolateral hair brush simplified. – 14. Ditto, dorsal view. – 15. Right pedipalp, ventral view. – 16. Ditto, dorsal view.



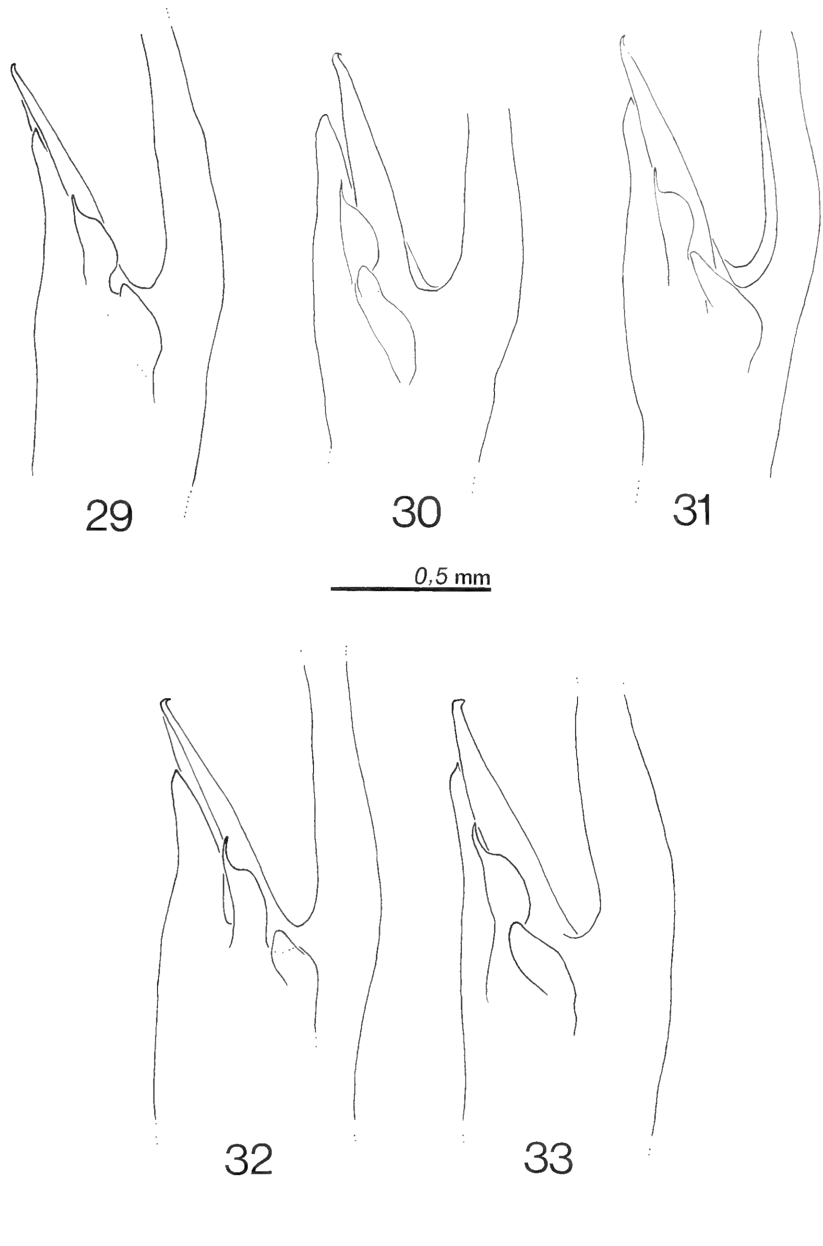
FIGS 17-23

Mesobuthus cyprius sp. n., male – 17. Right palpal femur, trichobothrial pattern, dorsal view. – 18. Right palpal patella, trichobothrial pattern, dorsal view. – 19. Ditto, retrolateral view; arrow and asterisk in Figs 18, 19 indicate the same trichobothria. – 20. Right chela, trichobothrial pattern, proventral view. – 21. Ditto, retrodorsal view. – 22. Distal part of fixed finger of right chela, inner side. – 23. Tip of movable finger of right chela, inner side.



FIGS 24-28

Mesobuthus cyprius sp. n., male legs. – 24. Left leg I, prolateral view. – 25. Ditto, retrolateral view. – 26. Left leg IV, prolateral view. – 27. Left tarsus I, ventral view; hairs omitted. – 28. Ditto, dorsal view.



FIGS 29-33

Mesobuthus gibbosus, lobes at truncal flexure of left hemispermatophore in specimens from different regions; same magnification as in Figs 8-9. – 29. Euboea (GR). – 30. Rhodes, Kolympia (GR). – 31. Rhodes, Monolithos (GR). – 32, 33. Selale (TR).

distinction is not reliable. On the one hand the mesosomal pattern is hardly visible in some animals, on the other hand specimens of *M. gibbosus* from the Peloponnesian peninsula (Mathia) and from Crete can also show this pigmentation pattern. The Peloponnesian individuals of M. gibbosus differ by a characteristic row of bristles on the mesosomal tergites, which cannot be found in *Mesobuthus cyprius* sp. n. There, only some scattered bristles, if any at all, do occur. Some of the Cretean specimens of *M. gibbosus* examined cannot be distinguished from *M. cyprius* sp. n. by means of external morphology, because they possess a similar pigmentation pattern and lack mesosomal bristle rows.

DISCUSSION

The allozyme data generally revealed a low genetic variability (Table 1), as already observed in earlier studies on scorpions of the family Euscorpiidae (Stockwell 1992; Gantenbein *et al.*, 1998, 1999). One exception is the population of *M. gibbosus* from the island of Rhodes which shows a higher level of heterozygosity as compared to the other *Mesobuthus* populations. This is mainly due to three gene loci (Ark, Gtdh, Sod) (Table 1). Specimens of *M. gibbosus* from Rhodes that are heterozygous at these three loci possess one allele, which is elsewhere only found in the samples from the Peloponnesus, and another allele, which is common in the Cretean and Anatolian populations. We speculate that this pattern indicates hybridization between western Aegean populations and eastern Aegean populations on the island of Rhodes. This hybridization may have resulted from secondary contact between the authochtonous Rhodes population and an introduced population of Greek origin.

The allozyme gene frequencies indicate that there are different population groups within *Mesobuthus*. In the NJ and ML tree, the Cyprus clade is separated from the other clades by a long branch (Figs 2-3). Both approaches clearly underline that the Cyprus scorpions have diverged considerably. Since the Biological Species Concept (BSC) (Mayr 1942) can hardly be applied to allopatric populations, it remains unsolved if the Cyprus population represents a separate species in this sense. Consequently, there are no objective arguments for the taxonomic rank of this population. However, our expectation that this island population remained isolated from the mainland populations since the colonisation 5.2 Myrs ago is supported by a high genetic divergence of the Cyprus clade and by the noninterchangeable morphology of the hemispermatophores. Taking these two arguments into account we, therefore, designate to the Cyprus population the rank of a species.

It is remarkable that *M. cyprius* sp. n. appears genetically distinct and highly differentiated, but can hardly be characterised by means of classical morphology. Such 'hidden' taxa are well known from other animal groups (e. g. mosquitos, polychaetes, myriapodes) (Narang *et al.*, 1989), especially on islands. The only characters that can be used for a morphological distinction are found in the hemispermatophores, in the mesosomal pigmentation pattern and in a lack of mesosomal bristle rows. The last character is a negative trait and presumably represents a plesiomorphic state as compared to most populations of *M. gibbosus*. The bristle row was found in specimens

of *M. gibbosus* from the Peloponnesus (Mathia) and from Rhodes (Petaloudes). The pigmentation pattern seems to be quite useful, because we found only limited variation there (but compare paragraph 'remarks' above). The taxonomic value of the pigmentation pattern was underlined by Lourenço (1983), who claimed that species with polymorphic colouration or pigmentation are an exception among buthids. As a conclusion, only a single reliable distinctive morphological character of *M. cyprius* sp. n. remains discriminant, i.e. the shape of the basal lobes of the hemispermatophores.

Based on a single male, Schenkel (1947) described a new variety of *M. gibbosus* from central Anatolia (collected along the road between Sivas and Amasya, Turkey). Kinzelbach (1975) elevated Schenkel's variety to subspecies rank. He distinguished *M. g. gibbosus* (Brullé, 1832) in the south of the Balkan Peninsula, Northern Sporades, Cyclades, from *M. g. anatolicus* (Schenkel 1947) living in Crete, Anatolia, and Cyprus, using differences in the number of pectinal teeth as the main character. Furthermore, he argued that these two subspecies were separated since the Miocene (12-25 Myrs BP). Kritscher (1993) refuted Kinzelbach's arguments for a separate subspecies *anatolicus* and rejected this taxon. The allozyme data now partially support the existence of two subspecies in Kinzelbach's sense. The Greek mainland populations are genetically slightly distinct from the Crete-Anatolian population group (Figs 2, 3). However, the Cyprus population (= *Mesobuthus cyprius* sp. n.) is genetically considerably more differentiated from all others, as discussed above. This fact contradicts the existence of *M. g. anatolicus* on Cyprus as proposed by Kinzelbach.

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Revue suisse de Zoologie
Muséum d'histoire naturelle
CP 6434
CH-1211 Genève 6
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de la
SOCIÉTÉ SUISSE DE ZOOLOGIE
et du
MUSÉUM D'HISTOIRE NATURELLE
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tome 107
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Etat trophique du lac de Morat indiqué par le zoobenthos: tendance 1980-1998

Claude LANG
Conservation de la faune, Marquisat 1, CH-1025 St-Sulpice, Suisse.
E-mail: claude.lang@sffn.vd.ch

Trophic state of Lake Morat indicated by the zoobenthos: the 1980-1998 trend. - Total phosphorus concentrations have strongly decreased between 1982 and 1998 in the water of Lake Morat (Switzerland). In response to this improvement, the numbers of tubificids (*Tubifex tubifex* and *Potamothrix hammoniensis* mostly) decreased in the deepest area (40-45 m), but the other species (*Limnodrilus profundicola* and *L. hoffmeisteri*) present therein, remained scarce. In contrast at a depth of 20 m, chironomid larvae (*Chironomus* and *Procladius*) and the tubificid *Potamothrix moldaviensis* became more abundant in 1998. These changes indicated a slow improvement of benthic conditions but, in 1998, the zoobenthos was always characteristic for a eutrophic lake.

Key-words: chironomid – eutrophication – indicator – lake – oligochaete - zoobenthos.

INTRODUCTION

Les concentrations en phosphore total dans l'eau du lac de Morat ont fortement diminué en réponse aux mesures d'assainissement prises dans le bassin versant, passant de 147 mg / m^3 en 1982 à 30 mg en 1998 (OPE, 1999). La baisse du phosphore devrait entraîner celle de la production des algues planctoniques, donc une diminution de la sédimentation organique, et par conséquence une meilleure oxygénation des couches d'eau profondes (Sas, 1989). La production des algues n'a pas été mesurée mais les concentrations en oxygène ont augmenté dans les eaux du fond pendant la stagnation estivale (OPE, 1999). Cette amélioration de l'oxygénation devrait faire sentir ses effets au niveau de la faune des sédiments profonds (faune benthique ou zoobenthos). Celle-ci se compose principalement (si on se limite à la macrofaune) d'oligochètes et de larves de chironomides (Diptera) dont les communautés d'espèces varient en fonction de l'état du lac et peuvent ainsi servir d'indicateurs (Johnson *et al.*, 1993).

Des conditions oligotrophes (peu de phosphore et beaucoup d'oxygène) prévalaient au début du siècle dans la plupart des grands lacs suisses (Sas, 1989). Les nombres d'individus appartenant à des espèces d'oligochètes et de chironomides

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indicatrices de ce type de conditions ont diminué en réponse à l'augmentation du phosphore entre 1960 et 1980, tant dans le Léman que dans le lac de Neuchâtel (Lang, 1998, 1999). Lorsque ce nutriment a diminué, les nombres d'individus de ces espèces ont augmenté à nouveau dans ces deux lacs, montrant ainsi que l'état des sédiments profonds s'améliorait. Les espèces oligotrophes ne sont plus présentes dans la zone profonde du lac de Morat où les espèces caractéristiques des lacs eutrophes constituent l'essentiel du zoobenthos entre 1980 et 1991 (Lang & Reymond, 1993).

En effet, ce lac est eutrophe depuis longtemps. En 1825 déjà (Jaag, 1948), l'eau du lac de Morat était devenue rouge à cause de la prolifération d'une cyanobactérie (*Oscillatoria rubescens*, appelée maintenant *Planktothrix rubescens* DC). Certains riverains, croyant que c'était le sang des soldats tués lors de la bataille de Morat en 1476 qui remontait à la surface, ont appelé ce phénomène Sang des Bourguignons. L'apparition de cet organisme révèle que l'état d'un lac commence à se dégrader (Sas, 1989). En 1936, la rareté de l'oxygène dans les couches d'eau profondes pendant la stagnation estivale indique que les algues prolifèrent en surface; le Sang des Bourguignons est toujours abondant, mais pas de façon continue (Rivier, 1936). La concentration en phosphore total qui est de 35 mg / m^3 en 1955, augmente jusqu'en 1982 avant de commencer à redescendre (Liechti, 1989). En 1972, le lac est qualifié d'eutrophe au vu de la composition chimique de ses sédiments (Davaud, 1976).

La présente étude cherche à évaluer et à interpréter la réponse du zoobenthos à la baisse des concentrations en phosphore entre 1982 et 1998 en termes d'amélioration de l'état biologique des sédiments profonds. En effet, le lac de Morat ne sera restauré que lorsque ses sédiments le seront puisqu'ils reçoivent, sous une forme ou une autre, tout ce qui est produit dans la colonne d'eau (Hakanson & Jansson, 1983). Si l'état des sédiments s'améliore, la densité des oligochètes devrait diminuer tandis que celle des larves de chironomides devrait augmenter (Wiederholm, 1980). De plus, la composition des espèces devrait se modifier au sein de ces deux groupes: les espèces très résistantes au manque d'oxygène devraient être remplacées peu à peu par celles qui prévalaient avant la phase d'eutrophisation intense (Lang, 1998).

STATIONS ET MÉTHODES

Le lac de Morat qui couvre une surface de 23 km^2, est relativement peu profond (profondeurs moyenne et maximale: 23 m et 45 m respectivement) ce qui explique sa sensibilité vis-à-vis de l'augmentation des concentrations en phosphore (Liechti, 1989). Son principal affluent, la Broye, contribue pour 87 % à ses apports en phosphore (OPE, 1999); c'est donc surtout l'état du bassin versant de cet affluent qui détermine celui du lac. Les mesures d'assainissement prises ont entraîné la baisse dans l'eau du lac des concentrations en phosphore total de 62 mg / m^3 en 1987 à 31 mg en 1996 (OPE, 1999). De ce fait, les concentrations moyennes en oxygène à 40 m de profondeur entre les mois de juillet et de novembre ont passé de 1.8 mg / l en 1987 à 3.6 mg / l en 1996; les valeurs extrêmes étant respectivement 1.5 à 2.9 mg et 2.1 à 4.9 mg. Les années antérieures à 1987 et postérieures à 1996 ne sont pas incluses dans la comparaison parce que la fréquence des mesures d'oxygène n'y est suffisante ni pour calculer une concentration moyenne pendant l'été ni pour estimer la durée de la

période où l'oxygène est rare. Pour cette raison, il n'est pas possible de comparer directement l'évolution des concentrations en oxygène entre 1980 et 1998 à celle du zoobenthos.

Entre 1980 et 1998, le zoobenthos du lac de Morat a été étudié dans 11 stations de prélèvements localisées entre 10 m et 45 m de profondeur (Fig. 1). A cela s'ajoutent, en 1994, 42 stations réparties régulièrement sur l'ensemble du lac et, en

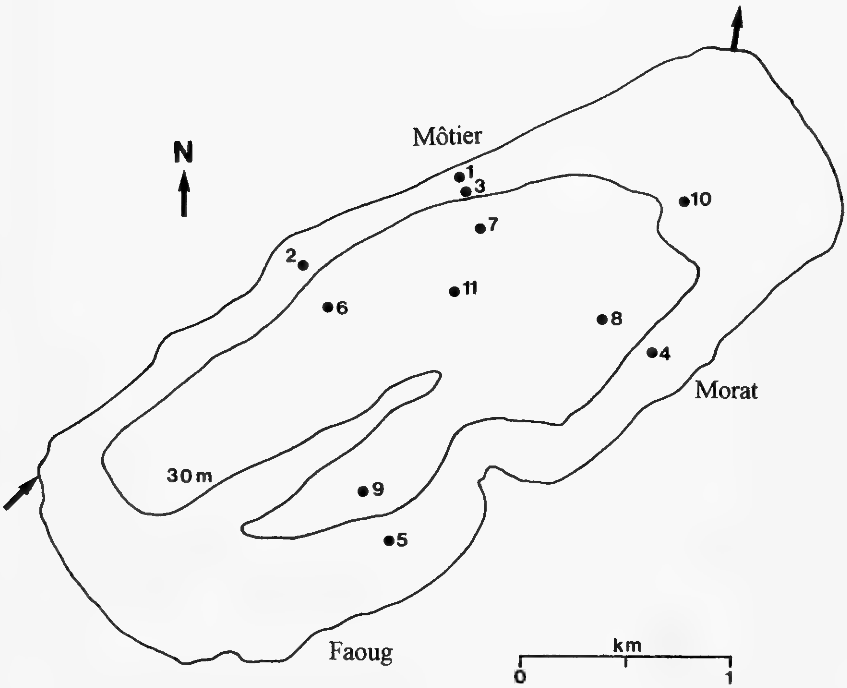

FIG. 1

Localisation des onze stations de prélèvements visitées entre 1980 et 1998 dans le lac de Morat. Les flèches indiquent les points d'entrée et de sortie de la Broye, le principal affluent.

1998, 15 stations distantes de 200 m les unes des autres, placées sur un transect qui va de la station 7 à la station 8. Dans chaque station, des carottes de sédiment de 16 cm^2 chacune ont été prélevées en nombre variable selon les années et les profondeurs (Tab. 1). Les prélèvements sont effectués au moyen d'un carottier, descendu depuis la surface à l'extrémité d'un cable, dans la plupart des stations, sauf dans les stations 1 et 3, visitées en plongée par l'auteur en 1987 et en 1998. Seule la station 1 est située dans la zone littorale (10 m), toutes les autres le sont dans la zone profonde (20 m à 45 m).

En laboratoire, le sédiment contenu dans chaque carotte est tamisé (ouverture de maille: 0.2 mm). Le refus du tamis est fixé au formol 5 %. La faune benthique est ensuite séparée du sédiment, sous une loupe lumineuse à l'aide de pinces fines. Les

TABLEAU 1

Fréquence et abondance (A) relatives (%) des espèces de tubificidés du lac de Morat en fonction de la profondeur, de la station et de l'année. Fréquences calculées seulement à partir des individus sexuellement matures. Fréquences 1980 pas comparables: + présence. Espèce 1 caractéristique des lacs mésotrophes; espèces 2 à 7 caractéristiques des lacs eutrophes (Milbrink 1973).

	Profondeur (m)													
Espèces	10	10	20	20	20	20	20	35	40	40	40	40	45	45
1. *Potamothrix moldaviensis* (Vejdovsky, Mrazek)	50	83					17							
2. *Ilyodrilus templetoni* (Southern)	33		20		6									
3. *Limnodrilus claparedeanus* Ratzel		17				6						7		
4. *Limnodrilus hoffmeisteri* Claparède		33			6	6					6			
5. *Limnodrilus profundicola* (Verrill)	17	17	10	+	25	19		31	+	12				
6. *Potamothrix hammoniensis* (Michaelsen)		83		+	25	6	100	48	+	87		13	60	5
7. *Tubifex tubifex* (Müller)		33	20	+	6	12	17	57	+	81	44	53	70	76
Espèce 1 (A)	12	19					2							
Espèces 3 à 5 (A)	22	29	25	25	30	27	29	11	7	2	1	2		
Espèces 2, 6, 7 (A)	66	52	75	75	70	73	69	89	93	98	99	98	100	100
Année	87	98	85	80	84	91	98	94	80	84	91	98	85	86
Jour et mois	28.4	31.3	8.7	30.7	25.6	25.6	31.3	21.6	30.7	25.6	25.6	23.6	8.7	28.7
Nbre carottes (16 cm2)	6	12	10	16	16	16	12	42	16	16	16	30	20	21
Nbre vers identifiés	40	48	24	121	125	59	56	402	169	306	143	134	170	174
Stations (fig. 1)	1	1	10	2-5	2-5	2-5	3	Fig. 3	6-9	6-9	6-9	7 à 8	11	11

oligochètes, les larves de chironomides et de *Chaoborus* sont comptés et pesés (biomasse), après passage sur du papier buvard pour enlever l'eau en excès. Tous les tubificidés (ou un sous-échantillon s'ils sont trop nombreux), dont le diamètre à l'état fixé dépasse 0.29 mm (Lang, 1998), sont montés entre lame et lamelle dans un milieu éclaircissant (Reymond, 1994) afin d'être identifié sous le microscope. Seuls les individus sexuellement matures des taxons présents dans le lac de Morat peuvent être identifiés jusqu'au niveau de l'espèce. Cependant, les immatures peuvent tout de même être classés dans des groupes d'espèces dont la valeur indicatrice est analogue (Lang, 1998). Nous distinguons ainsi les espèces caractéristiques des lacs oligotrophes, mésotrophes ou eutrophes. La fréquence relative d'une espèce s'exprime comme le pourcentage de carottes dans lesquelles cette espèce est présente. L'abondance relative d'une espèce se définit comme le nombre d'individus de cette espèce rapporté, sous forme de pourcentage, au nombre total d'individus identifiés dans une carotte ou un ensemble de carottes.

De 1984 à 1998, les résultats sont analysés carotte par carotte, contrairement à 1980, où les 4 carottes prises dans chacune des 8 stations visitées cette année-là sont cumulées. De plus, la biomasse n'a pas été mesurée en 1980. Pour ces raisons, les

résultats de 1980 ne peuvent pas être inclus dans toutes les comparaisons effectuées entre les années. Les seules campagnes de prélèvements vraiment comparables entre elles à tous les points de vue sont celles effectuées en 1984, 1991 et en 1998 à 20 m et 40 m de profondeur.

La biomasse du zoobenthos (g/m^2) peut être calculée à partir des concentrations en phosphore total (mg/m^3) en utilisant une relation empirique établie dans d'autres lacs (Hanson & Peters, 1984):

$$\mathrm{Log}_{10}\ \mathrm{biomasse} = 0.708\ \log_{10}\ \mathrm{phosphore} + 0.092$$

La concentration moyenne du phosphore, calculée sur les cinq années précédant le prélèvement du zoobenthos, est utilisée dans cette expression pour tenir compte du fait que le zoobenthos réagit souvent avec un temps de latence à la baisse du phosphore (Lang, 1998). Si la biomasse observée est proche de la biomasse calculée, cela signifie qu'il n'y a pas de décalage entre l'état trophique du sédiment et celui de l'eau. Ce type de relation empirique permet de replacer l'évolution trophique d'un lac particulier dans un contexte plus général et de mettre ainsi en évidence d'éventuelles anomalies (Lang, 1998).

RÉSULTATS

Dans le lac de Morat, la diversité du zoobenthos diminue avec la profondeur (Tab. 1) ce qui reflète la baisse des concentrations en oxygène (OPE, 1999). A 40 m et 45 m de fond, le zoobenthos se compose presque exclusivement de deux espèces de tubificidés, très résistantes au manque d'oxygène, dont la dominance numérique caractérise les lacs eutrophes: *Potamothrix hammoniensis* et *Tubifex tubifex* (Milbrink, 1973). Le pourcentage de ces deux espèces dans les communautés d'oligochètes ne change guère à 40 m entre 1980 et 1998. A 20 m de profondeur, le pourcentage des espèces du genre *Limnodrilus* augmente par rapport à 40 m, mais reste assez constant entre 1980 et 1998. Notons en 1998 la présence à 20 m de *Potamothrix moldaviensis*, une espèce plutôt caractéristique des lacs mésotrophes (Milbrink, 1973), qui est relativement abondante à 10 m, tant en 1987 qu'en 1998. Les cinq premières espèces du tableau 1 sont présentes dans le Léman jusqu'à 150 m de profondeur au moins (Lang, 1998), ce qui montre que ce n'est pas ce facteur qui limite leur distribution verticale dans le lac de Morat, mais plutôt le manque d'oxygène.

A 40 m de profondeur, la biomasse du zoobenthos ne change pas entre 1984 et 1998 (Tab. 2), mais le nombre de tubificidés diminue significativement (test de Kruskal Wallis: $P = 0.084$ et $P = 0.007$ respectivement). A 20 m de fond, la biomasse du zoobenthos augmente entre 1984 et 1998. Cette augmentation est surtout le fait des larves de chironomides qui constituent en 1998 le 54 % de la biomasse. Seuls les genres *Chironomus* et *Procladius*, résistants au manque d'oxygène (Brinkhurst, 1974), sont présents et leur abondance est la même (1500 individus/m^2). Une tendance semblable s'observe en1998 à 10 m de profondeur: les chironomides forment le 43 % de la biomasse, *Chironomus* et *Procladius* sont dominants. Mis à part 1998 (à 10 m et 20 m), les chironomides ne représentent qu'une petite partie de la biomasse totale dans la zone profonde du lac de Morat qui se caractérise par la prédominance des tubificidés. Notons enfin la présence de quelques larves de *Chaoborus* à 40 m de profondeur.

TABLEAU 2

Biomasse moyenne (g / m^2) du zoobenthos et nombre moyen d'oligochètes par m^2 en fonction de la profondeur et de l'année dans cinq lacs: Morat, Léman, Neuchâtel, Joux, Bret. Sources: cette étude, Lang 1998 et 1999, résultats non publiés.

Lac	Profondeur (m)	Année	n[1)]	Biomasse [2)] Moy.	ESM	Max.	Nombre Moy.	ESM	Max.
Morat	10	1987	6	13.5	3.1	24	30104	3016	39375
		1998	12	24.1	3.2	38	12604	1873	27500
	20	1980	16	- [3)]	-	-	23750	-	-
		1984	16	9.3	2.6	45	18085	2374	41250
		1991	16	7.8	1.5	19	11289	1341	25000
		1998	12	49.7	5.4	82	30677	3439	56875
	35	1994	42	43.2	8.5	356	49405	6074	245625
	40	1980	16	-	-	-	29375	-	-
		1984	16	22.8	2.9	56	26875	3159	62500
		1991	16	19.9	3.9	66	21679	3408	55000
		1998	30	21.1	4.8	108	21541	5079	125625
	45	1985	20	33.1	6.5	119	21312	3212	53750
		1986	21	19.3	3.2	62	20833	2587	52500
Léman	40	1991	192	24.0	1.6	219	24687	2111	274375
		1996	170	17.3	0.6	47	12092	585	48125
	60	1994	159	13.5	0.6	38	20243	929	58750
		1999	159	11.6	0.7	57	12448	785	71875
Neuchâtel	40	1992	171	10.2	0.5	35	9181	570	61250
		1997	175	9.4	0.5	32	8546	569	45625
Joux	25	1998	450	52.1	1.5	186	39164	1001	230000
Bret	20	1998	35	21.8	2.3	52	929	202	4375
Léman	270	1998	25	4.0	0.8	19	5500	686	12500

1) nbre de carottes de 16 cm^2

2) Moy. moyenne, ESM erreur standard de la moyenne, Max. valeur maximale.

3) Résultats manquent.

La campagne de prélèvements effectuée en 1994 montre (Fig. 2 et 3) la répartition et la composition du zoobenthos dans l'ensemble la zone profonde du lac de Morat. Les valeurs de la biomasse du zoobenthos qui sont plus élevées dans la zone du lac influencée directement par les apports organiques de la Broye, le principal affluent (70 % des apports en eau, Liechti, 1989), diminuent en général au fur et à mesure que l'on s'en éloigne, tout comme les taux de sédimentation organique (Davaud, 1976). *Tubifex tubifex* et *Potamothrix hammoniensis* constituent l'essentiel

tant des tubificidés (89 % des individus en moyenne) que du zoobenthos. Les autres espèces de tubificidés du genre *Limnodrilus* se rencontrent surtout à la périphérie de la zone étudiée où la profondeur diminue. Les larves de chironomides ne sont présentes que dans 6 des 42 stations visitées et, en nombre d'individus (un individu seulement dans chacune des 6 stations), elles ne représentent que le 0.2 % du nombre des tubificidés. Cependant, comme les prélèvements ont été effectués le 14 et le 21 juin, donc à la fin de la période d'émergence des chironomides, l'abondance des larves est probablement sous-estimée. Des prélèvements effectués en avril seraient plus représentatifs à cet égard.

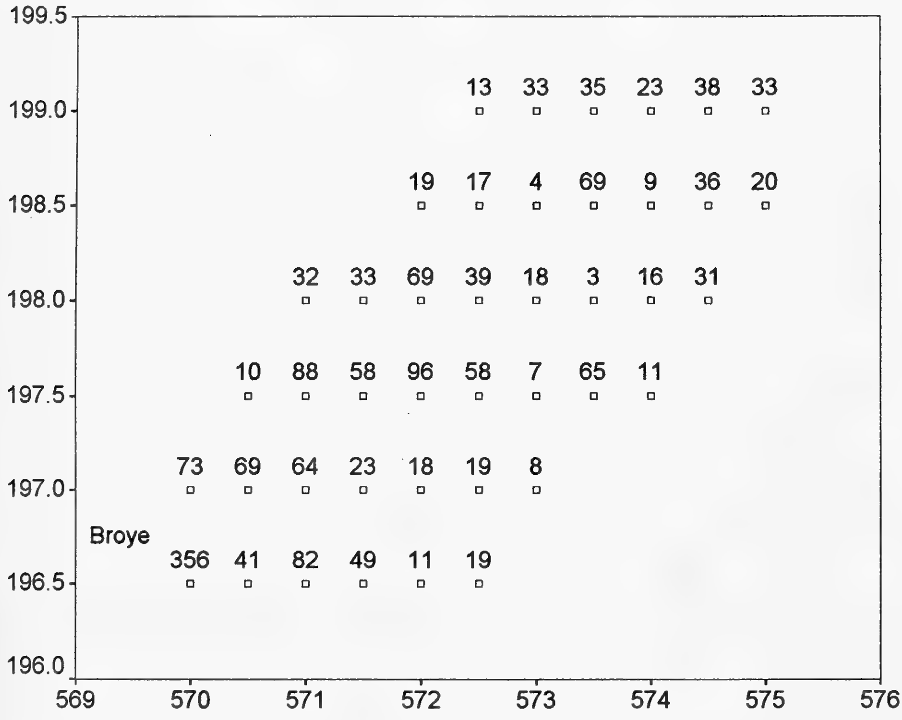

FIG. 2

Répartition géographique de la biomasse du zoobenthos (g /m^2) dans le lac de Morat en 1994. Les coordonnées géographiques de la carte nationale de la Suisse sont indiquées en x et en y.

La biomasse moyenne du zoobenthos est de 43.2 g / m^2 dans les 42 stations visitées en 1994 (Fig. 2); la biomasse médiane qui ne prend pas en compte les stations très influencées par les apports de la Broye, est de 32.2 g / m^2. Ces deux valeurs observées sont bien supérieures à 16.5 g / m^2, la biomasse calculée à partir de la moyenne (39 mg / m^3) des concentrations en phosphore dans l'eau entre 1989 et 1993 (voir Stations et méthodes). Par contre, la biomasse médiane observée en 1994 est très proche de 35.2 g / m^2, la biomasse calculée à partir de la moyenne des concentrations en phosphore mesurées entre 1982 et 1986 (113.4 mg / m^3). Cette différence montre que la biomasse du zoobenthos réagit lentement à la baisse du phosphore si bien que

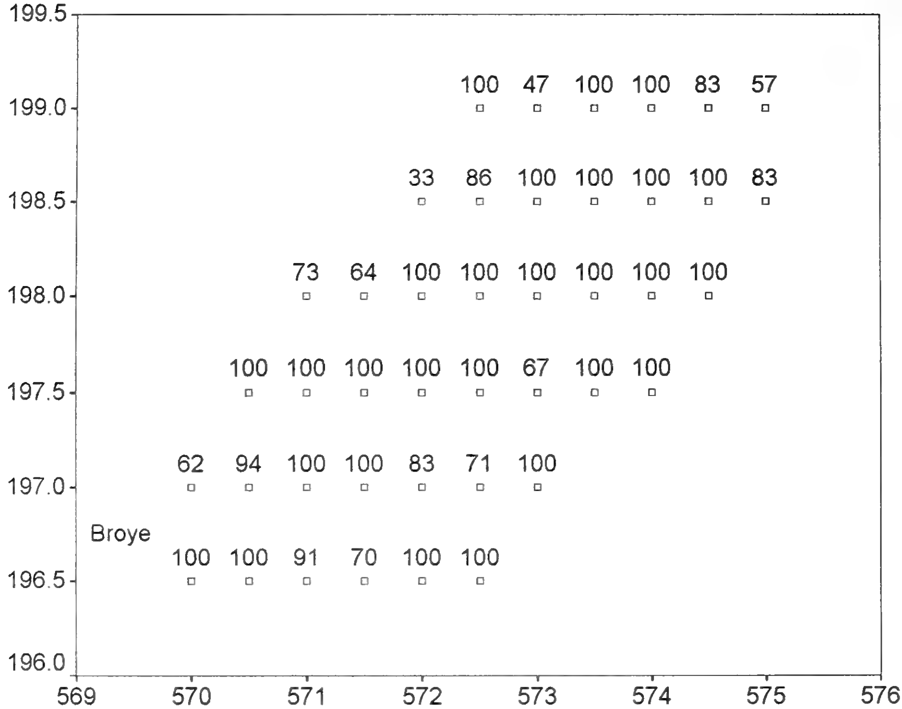

FIG. 3

Répartition géographique du pourcentage de *Tubifex tubifex* et de *Potamothrix hammoniensis* dans les communautés de tubificidés du lac de Morat en 1994.

les sédiments restent capables en 1994 de nourrir des populations benthiques qui correspondent encore au niveau de productivité observé dix ans plus tôt dans l'eau du lac.

DISCUSSION

Le lac de Morat est un des premiers lacs suisses dont l'état s'est dégradé sous l'influence des activités humaines (Jaag, 1948). La prolifération du Sang des Bourguignons en 1825 indique le début de cette dégradation. Une intensification des activités agricoles dans le bassin versant de la Broye, le principal affluent du lac, pourrait en avoir été la cause, comme c'est le cas depuis le moyen âge déjà pour de nombreux lacs d'Europe (Anderson, 1995). Signalons par exemple la culture du tabac qui s'est développée entre 1719 et 1819 dans la plaine de la Broye (Chuard & Dessemontet, 1972). De même, la production de blé a augmenté de 38 % entre 1707-1709 et 1787-1789 dans les balliages de Payerne et d'Avenches qui englobaient la partie inférieure du bassin versant (Chevallaz, 1949). Cet auteur fait également remarquer que l'agriculture vaudoise s'est fortement développée à partir de 1803 grâce à la suppression des usages et des structures contraignants de l'Ancien Régime.

Cette évolution rapide des pratiques agricoles s'effectue dans un contexte météorologique particulier. Les années 1816 et 1817 se caractérisent en effet par des pluies et des inondations exceptionnelles (Pfister, 1985). Celles-ci résultent du bouleversement climatique engendré par la présence, dans la haute atmosphère, des poussières provenant de l'éruption en 1815 du volcan indonésien Tambora (Whyte, 1995). Ces pluies, tombant sur les sols du bassin versant du lac de Morat, cultivés de façon plus intensive, en ont probablement lessivé les nutriments, créant ainsi les conditions qui ont provoqué en 1825 la prolifération du Sang des Bourguignons. Cette longue histoire de dégradation (plus de 150 ans) laisse supposer que la restauration biologique du lac de Morat prendra plus de temps que celle du Léman ou du lac de Neuchâtel où la phase de détérioration n'a duré qu'une trentaine d'années (Lang, 1998, 1999).

Malgré la baisse spectaculaire des concentrations en phosphore dans l'eau du lac de Morat, la composition du phytoplancton et son abondance, ainsi que celles du périphyton épilithique, restent caractéristiques d'un lac eutrophe en 1988 et en 1989 (Reymond & Straub, 1993). De même, le zoobenthos ne se modifie pas de façon fondamentale entre 1980 et 1998, tout au moins dans la zone profonde, seule étudiée en détails. Les deux espèces de tubificidés qui restent les plus abondantes entre 1980 et 1998, *Tubifex tubifex* et *Potamothrix hammoniensis*, étaient déjà les seules présentes en 1935 dans la zone la plus profonde du lac (Rivier, 1936). A cette époque, elles colonisaient en petit nombre le fond du lac en compagnie des larves de *Chaoborus* qui étaient relativement abondantes. Ce genre de faune se rencontre dans des lacs très eutrophes, où le manque d'oxygène persiste pendant des mois. Dans ce type de situation, l'abondance des tubificidés qui vivent constamment en contact avec le fond du lac, diminue davantage que celle des *Chaoborus* qui peuvent migrer chaque nuit vers la surface et les couches oxygénées (Brinkhurst, 1974). C'est la situation observée en 1998 dans le lac de Bret à 20 m de profondeur où *Chaoborus* constitue le 98 % de la biomasse (Tab. 2). Lorsque le lac est profond, les *Chaoborus* sont absents; dans le Léman par exemple, seuls les tubificidés sont présents entre 270 m et 300 m de fond et leur biomasse est faible à cause du manque d'oxgène qui caractérise cette zone (Lang, 1998). En 1972 comme en 1936, les sédiments profonds du lac de Morat semblaient presque dépourvus de faune, mis à part les *Chaoborus* et quelques tubificidés (Davaud, 1976). Entre 1980 et 1998, les tubificidés sont devenus abondants et les *Chaoborus* rares, ce qui tendrait à montrer que l'état biologique des sédiments s'est amélioré par rapport à la situation précédente. Toutefois, comme celle-ci n'est pas décrite de façon quantitative dans les travaux de Rivier et de Davaud, l'interprétation de la tendance peut être mise en doute.

Lorsque l'état d'un lac s'améliore après un épisode d'eutrophisation, la densité des larves de chironomides augmente tandis que celle des oligochètes diminue (Wiederholm, 1980). Cette tendance s'observe en 1998 dans le lac de Morat: à 10 m et à 20 m de profondeur en ce qui concerne les chironomides, à 40 m en ce qui concerne les tubificidés. Remarquons toutefois que l'abondance moyenne des oligochètes en 1998 à 40 m est plus du double de celles observées à la même profondeur dans le lac de Neuchâtel en 1992 et 1997 (Tab. 2); les valeurs du Léman à 40 m et à 60 m de profondeur se situent entre ces deux extrêmes. Cette séquence des abondances – Morat, Léman, Neuchâtel – reflète la décroissance des concentrations en

phosphore entre ces trois lacs. Cependant, il existe des exceptions à cette règle. Dans le lac de Joux par exemple, malgré la baisse du phosphore, la biomasse du zoobenthos et l'abondance des tubificidés restent élevées à cause de la présence presque continue du Sang des Bourguignons qui sédimente en masse sur le fond du lac entre 1980 et 1998. Une fois installé dans un lac, cet organisme peut en effet s'y maintenir malgré les mesures d'assainissement prises (Sas, 1989). Son retour en force dans le lac de Morat n'est d'ailleurs pas exclu.

L'amélioration constatée dans le lac de Morat est plus marquée à faible qu'à grande profondeur. De ce fait, des prélèvements de zoobenthos concentrés sur les bords de la zone profonde (entre 15 m et 30 m) auraient probablement mieux mis en évidence la restauration de l'état des sédiments que le programme suivi. Une autre stratégie possible consiste à augmenter l'intervalle de temps entre les campagnes de prélèvements de manière à ce que le zoobenthos puisse répondre de façon plus claire à la baisse du phosphore. Par exemple, la campagne de 1994 qui couvre l'ensemble de la zone profonde (Fig. 2 et 3), pourrait être refaite en 2004, si possible en avril avant l'émergence des chironomides. Si ces dix ans d'amélioration chimique ont eu un effet positif au niveau du sédiment, les larves de chironomides devraient devenir plus nombreuses et recoloniser l'ensemble de la zone profonde, la baisse de l'abondance des tubificidés devrait se poursuivre et la dominance de *Tubifex tubifex* et *Potamothrix hammoniensis* devrait diminuer au profit d'autres espèces moins résistantes au manque d'oxygène. La colonisation par *Potamothrix moldaviensis*, espèce indicatrice de conditions mésotrophes, des sédiments situés à 45 m de profondeur montrerait que le lac de Morat est vraiment en voie de restauration.

Si la baisse du phosphore se poursuit, le retour des espèces indicatrices de conditions oligotrophes, comme dans le Léman et le lac de Neuchâtel (Lang, 1998, 1999), n'est pas exclu à long terme. L'exemple du lac Esrom montre que celles-ci peuvent en effet rester présentes à très faible profondeur (entre 0.5 m et 1.5 m) dans le littoral d'un lac eutrophe, comme c'est le cas du lumbriculidé *Stylodrilus heringianus* (Dall *et al.*, 1990). Signalons à ce propos qu'en 1905 *Spirosperma ferox* et *Psammoryctides barbatus*, deux espèces de tubificidés indicatrices de conditions oligo-mésotrophes (Milbrink, 1973), étaient présentes à 4 m de profondeur dans le lac de Morat (Piguet, 1906). Si elles ont subsisté à très faible profondeur comme c'est probable, elles pourraient graduellement recoloniser le lac au fur et à mesure des progrès de la restauration.

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A new species of *Astyanax* (Characiformes, Characidae) from Uruguay river basin in Argentina, with remarks on hook presence in Characidae

María de las Mercedes AZPELICUETA[1] and José O. GARCIA[2]

[1] Dep. Científico Zoología de Vertebrados, Fac. de Ciencias Naturales y Museo de La Plata, Paseo del Bosque, 1900 La Plata, Argentina.

[2] Fac. de Cs. Exactas y Naturales, Universidad Nacional de Misiones, Rivadavia 2370, 3300 Posadas, Argentina.

A new species of *Astyanax* (Characiformes, Characidae) from Uruguay river basin in Argentina, with remarks on hook presence in Characidae. - In the present paper the new species *Astyanax ojiara* sp. n. is described, from the headwaters of Yabotí river, an affluent of Uruguay river in the province of Misiones, Argentinean northeast. A combination of characters differentiates the new species from other congeners: one heptacuspid maxillary teeth; teeth of inner premaxillary row gently expanded distally; 7-9 dentary teeth decreasing in size anteroposteriorly; males with hooks in all fins; large males with pelvic axillary scale bearing 1 to 8 hooks; 36-38 perforated scales in lateral line; 20-23 branched anal-fin rays. Number of scales in the lateral line and branched anal-fin rays, humeral spot, and low body of *Astyanax ojiara* sp. n. resemble those of *A. eigenmanniorum*, but maxillary, premaxillary and dentary teeth differ in both species. The disposition of the dentary teeth is also similar in *A. taeniatus* and *A. giton* but *A. ojiara* sp. n. has one heptacuspid maxillary tooth.

Key-words: Characiformes - Characidae - *Astyanax* - new species - Uruguay river.

INTRODUCTION

In the last years, the genus *Astyanax* was not revised and an accurate definition of the genus is still pendant. Eigenmann (1921, 1927) analised the genus and, subsequently, many authors followed his results. Géry (1977) provided an arrangement of the species in groups, and identification keys. Recently, Zanata (1997) erected a new genus - *Jupiaba* - for many species previously known as *Astyanax* or *Deuterodon*. *Jupiaba* is defined by the presence of a diagnostic pelvic bone, with unique disposition of muscles. The taxonomic status of some species of the genus *Astyanax* is not completely clear and the interrelationships of the species remain unresolved. A detailed revision of the remaining nominal species of *Astyanax* is necessary.

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In the río de la Plata basin, about twenty nominal species of *Astyanax* have been recorded, although the records of some species are doubtful. In the southwest of the Brazilian shield, the main course of the río Uruguay flows from East to West, turning to the southwest and ending in the río de la Plata. Some affluents of the river originate from the Sierra de Misiones, which reach about 800 m a.s.l., and presently constitute an effective barrier between waters of the Uruguay and Paraná rivers, in northeastern Argentina. The arroyo Yabotí comes from the highest area of Sierra de Misiones; in one of its headwaters, the arroyo Benítez, a new species of *Astyanax* was collected in the vicinity of the city of San Pedro. The description of the new species is presented in this paper.

MATERIAL AND METHODS

The specimens examined in this study were cleared and counterstained (C&S) following Taylor & Van Dyke (1985). Measurements are straight distances taken with calliper to nearest 0.1 mm. Material is deposited in the Field Museum of Natural History, Chicago (FMNH); Muséum d'histoire naturelle de Genève, Genève (MHNG); Facultad de Ciencias Naturales y Museo de La Plata, La Plata (MLP); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP).

Comparative material (SL in mm). *Astyanax eigenmanniorum* (Cope, 1876): MLP 5202, 5 ex., 56.5-68.5, Argentina, Córdoba, río Primero frente a Capilla de los Remedios; MLP 9160, 6 ex., 36.8-80.2, Argentina, Buenos Aires, Los Talas. Cleared and stained material: Personal collection of MA. *Astyanax abramis* (Jenyns, 1842): 2 ex., 74.5-92.0, Argentina, Buenos Aires, río de la Plata en Punta Lara; 2 ex., 80.6-98.8, Argentina, Misiones, río Piray-Miní. *Astyanax alburnus* (Hensel, 1870): 5 ex., 40.5-47.2 , Uruguay, río Yaguarón. *Astyanax alleni* (Eigenmann and McAtee, 1907): 2 ex., 62.4-72.9, Argentina, Corrientes, río Riachuelo; 1 ex., 66.0, same collecting data. *Astyanax* cf. *asuncionensis* Géry, 1972: 2 ex., 28.0-37.6, Argentina, Santa Fe, Isla Los Sapos; 2 ex., 80.4-92.7, Argentina, Misiones, río Uruguay en San Isidro. *Astyanax eigenmanniorum*: 2 ex., 17.7-33.0, Argentina, Buenos Aires, desembocadura del río Colorado; 2 ex., 28.0-30.5, Argentina, Buenos Aires, Laguna de Gómez; 1 ex., 60.3, Argentina, Buenos Aires, río de la Plata; 4 ex., 51.5-82.1, Argentina, Misiones, arroyo Piray-Miní; 1 ex., 45.0, Brasil, Rio Grande do Sul, Viamão, açude Charolês; *Astyanax* cf. *fasciatus* (Cuvier, 1819): 2 ex., 91.0-106.5, Argentina, Misiones, río Uruguay en San Isidro. *Astyanax ojiara* sp. n.: 3 females, 46.2-63.0; 7 males, 37.8-58.0, Argentina, Misiones, arroyo Benítez.

TAXONOMY

Astyanax ojiara sp. n. Figs 1-13, table 1

Holotype (Fig. 1). MLP 9470, male, 50.5 mm SL, Argentina, province of Misiones, arroyo Benítez, headwaters of río Yaboty, an affluent of río Uruguay, coll. J. O. García, May 1983.

Paratypes. (Collecting data as holotype). MLP 9471, 2 males, 38.0-45.0 mm. MLP 9472, 12 females, 39.8-72.0 mm. MHNG 2605.67, 10 males (measured); MHNG 2606.35, 3 females, 44.0-53.5 mm, (not measured). FMNH 98319, 5 ex. MZUSP 40255, 5 ex.

Diagnosis

The species is distinguished by a combination of characters: one maxillary teeth with seven small cusps; teeth of inner premaxillary row gently expanded distally; 7-9 dentary teeth decreasing in size anteroposteriorly; large males with hooks in all fins; large males with 1 to 8 hooks in the pelvic axillary scale; 36-38 perforated scales in the lateral series; and iv-v,20-23 anal-fin rays. Also, presence of humeral spot vertically elongated, a second faint humeral spot, caudal spot continued on middle caudal rays, and low body depth help to differentiate the new species.

Description

Morphometrics of holotype and 24 paratypes are presented in table 1. *Astyanax* with low body (Fig. 1), maximum body depth at dorsal-fin origin. Dorsal profile of body slightly convex from snout to posterior tip of supraoccipital process, angled behind supraoccipital, strongly marked in medium sized and large females. Dorsal profile of body gently curved from this point to origin of dorsal fin; in large females, that portion almost straight; slanted ventrally from dorsal-fin origin to caudal peduncle. Dorsal profile of caudal peduncle straight; ventral profile slightly convex or straight. Ventral profile of body slightly curved from tip of snout to pelvic-fin origin, straight between this point and anal-fin origin, and slanted dorsally to caudal peduncle. Body rounded between pectoral and pelvic fins. Body laterally compressed between pelvic and anal fins.

Dorsal-fin origin nearer tip of snout than base of caudal-fin rays, equally distant in some small specimens. Pelvic-fin origin anterior to vertical through dorsal fin-origin. Adipose fin anterior to bases of last branched anal-fin rays. Tip of pectoral fin falling near, sometimes surpassing, pelvic-fin origin; in large females, tip of pectoral fin far from that origin. Tip of pelvic fin reaching anal-fin origin in males; in females, pelvic-fin tip far from that origin, even in many small specimens.

Dorsal fin iii, 9; posterior margin of dorsal fin slightly rounded, first branched dorsal-fin ray longest. In males, all dorsal-fin rays, excluded last one and unbranched rays, with slender hooks, directed outward, most of them curved ventrally, more abundant on posterior branch of each ray (Fig. 2), usually, one pair on each segment. Few hooks developed on ray tips of small specimens.

Anal-fin iv-v, 20-23 (holotype 21). Posterior margin almost straight in males; in females, first five branched rays produced forming a small lobe. Anal fin of all males bearing hooks directed posteriorly and outward, slightly curved dorsally. Large specimens with hooks on last branched anal-fin ray and also on largest unbranched ray. Hooks placed on all branches of the ray (Fig. 3), sometimes two or three pairs on each segment.

Caudal fin bearing 10-12 dorsal and 9-10 ventral procurrent rays; one unbranched and 9 branched principal rays in upper lobe; 8 branched and 1 unbranched principal rays in lower lobe. Usually, caudal lobes similar in size; sometimes, lower one slightly longer. Few hooks occurring on distal tips of middle caudal-fin rays in males (Fig. 4). In some specimens, few hooks scattered on all fin rays, included principal unbranched one. Hooks directed outward, most of them on lower lobe curved dorsally

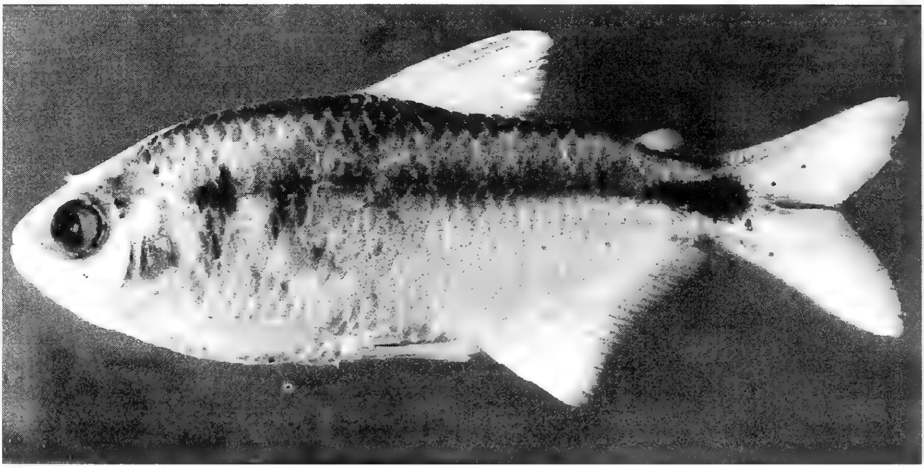


FIG. 1

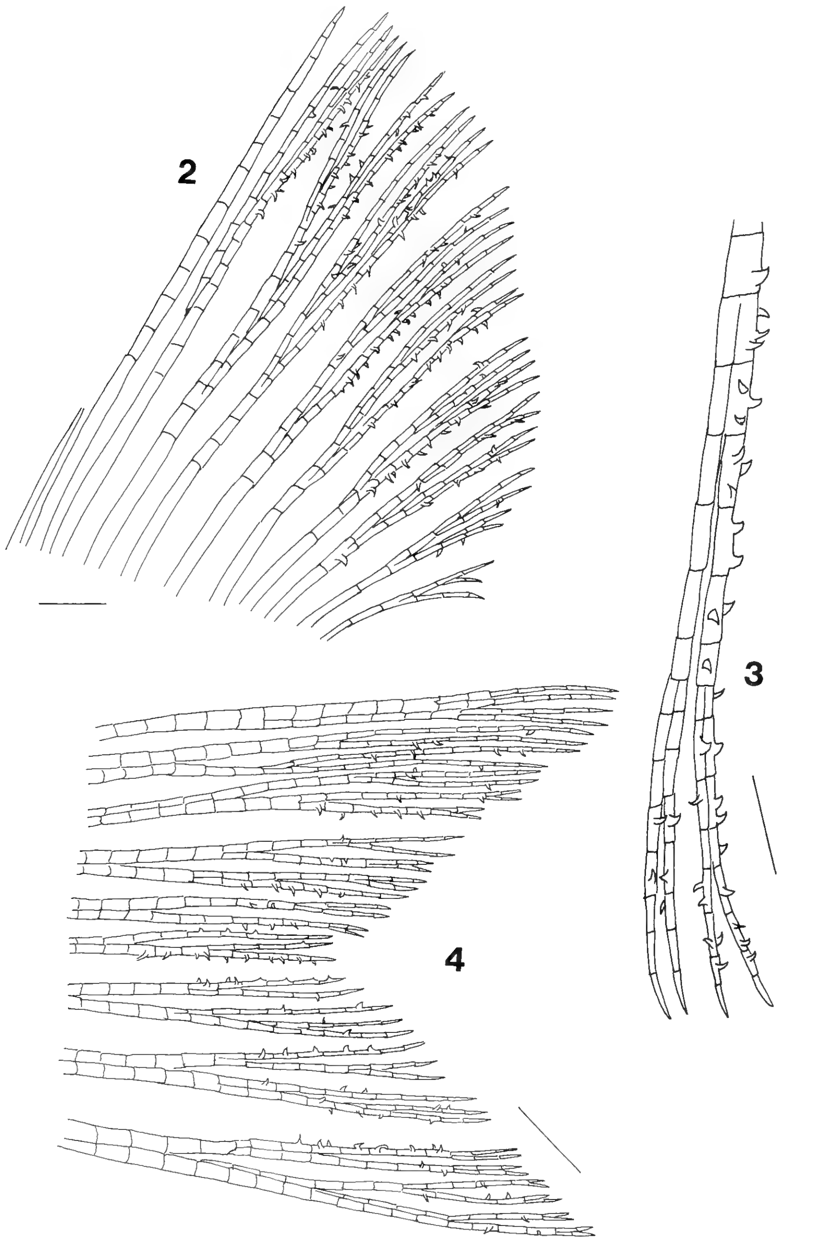
Astyanax ojiara new species, holotype, MLP 9470, male, SL 50.5 mm, Argentina, province of Misiones, arroyo Benítez, headwaters of río Yaboty, an affluent of río Uruguay.

and those ones of upper lobe curved ventrally. Some small specimens with 2 or 3 pairs of hooks only; one 43.0 mm SL male without hooks.

Pectoral-fin i, 10-13 (holotype i, 12), rays bearing hooks of different size in males. In medium sized and large specimens hooks developed on first unbranched ray and until 9 branched rays. Sometimes more than one pair of hooks on each segment, some of them directed dorsally and other ones ventrally, most of them directed inward (Fig. 5). Very few hooks developed in small specimens.

Pelvic fin i, 7; hooks developed on branched rays, occasionally on first unbranched ray also in large specimens (Fig. 6). One or two pairs of hooks on each segment, in different branches of ray, most of them directed inward, slightly curved anteriorly. Usually, one ray with scarce hooks in small specimens.

Head length moderate, mouth terminal, horizontal; snout short. Lower jaw slightly longer. Premaxilla with short ascending process, bearing two series of teeth. Usually, 3 pentacuspid or tricuspid teeth in outer series, sometimes two or four teeth, central cusp larger. Inner series of premaxillary teeth consisting of 5 teeth, gently expanded distally, slightly compressed at distal tips (Fig. 8). Symphysial tooth narrower and deeper, with 4 or 6 cusps. Second tooth widest, with 7 cusps. Third and fourth teeth with 6-7 cusps. Fifth tooth smaller, with 5 cusps. In all teeth, central cusp slightly larger than remaining ones. Maxilla short, scarcely lobed posteriorly, almost reaching or scarcely surpassing vertical through anterior orbital margin. One compressed maxillary tooth, with seven small cusps (Fig. 9). Few specimens (about 8 %) with two maxillary teeth, one of them heptacuspid. Dentary bearing 7 to 9 (usually 8) teeth with broad bases, decreasing in size anteroposteriorly. Symphysial tooth narrower, with 5-6 cusps. Second tooth widest. Second, third and fourth teeth with 5-7 cusps. Fifth tooth with 3-5



FIGS 2-4

Astyanax ojiara, left view. 2: dorsal fin, SL 44.5 mm, scale= 1 mm; 3: detail of hooks on third branched anal-fin ray, SL 39.6 mm, scale= 0.5 mm; 4: detail of hooks on middle caudal-fin rays, SL 39.6 mm, scale= 1 mm.

cusps, sixth and seventh teeth with 1 to 3 cusps; eighth tooth - and nineth one when present - always conic (Fig. 10).

Eye small, interorbital wide. Six infraorbitals well developed; third infraorbital almost contacting sensory tube of preopercle. Anterior fontanelle triangular, widening posteriorly; posterior fontanel long, extending onto supraoccipital process base.

Scales cycloid, crenate. Lateral series with 36-38 perforated scales (holotype with 37, one specimen with 39). Lateral line running on lower half of caudal peduncle, ending in a long tube without lamina, between caudal rays. Five scales between dorsal-fin origin and lateral line; 5 between lateral line and ventral-fin origin. Thirteen or fourteen scales around caudal peduncle. Eleven or twelve scales forming a regular row between supraoccipital process and dorsal-fin origin; sometimes, 14 scales in an irregular row. Ten to twelve (until 14) rectangular scales placed on anal-fin base, covering all unbranched and twelve branched anal-fin rays. Scales placed on basal fifth of caudal lobes. A narrow axillary scale present dorsal to pelvic-fin insertion, oval, as long as one third of pelvic fin sometimes. Axillary scale bearing two hooks in its posterior inner area in medium and large males; although, a high number of hooks developed (8 in largest male, 56 mm SL, Figs 11-13). Young males with a ridge in that area of scale.

In ten cleared and stained specimens, first arch bearing 17-19 gill-rakers: 2 on hypobranchial, 8 on ceratobranchial, 1 on cartilage, and 6 to 8 on epibranchial. Vertebral counts including Weberian apparatus and CU1+PU1 as one element: 32 (1 sp.), 33 (2 sp.), and 34 (7 sp.).

Coloration of alcohol preserved specimens: Background light brown, dorsal region of flanks and head darker. A humeral spot well developed, dorsoventrally expanded, at level of pectoral-fin origin. A second lateral spot faint and smaller, usually rounded. A dark lateral band with different intensity in coloration and width crossing flanks. A deep and very narrow line of chromatophores runnig from humeral spot to base of middle caudal-fin rays. Most specimens with dark chromatophores on inner opercular surface forming a spot.

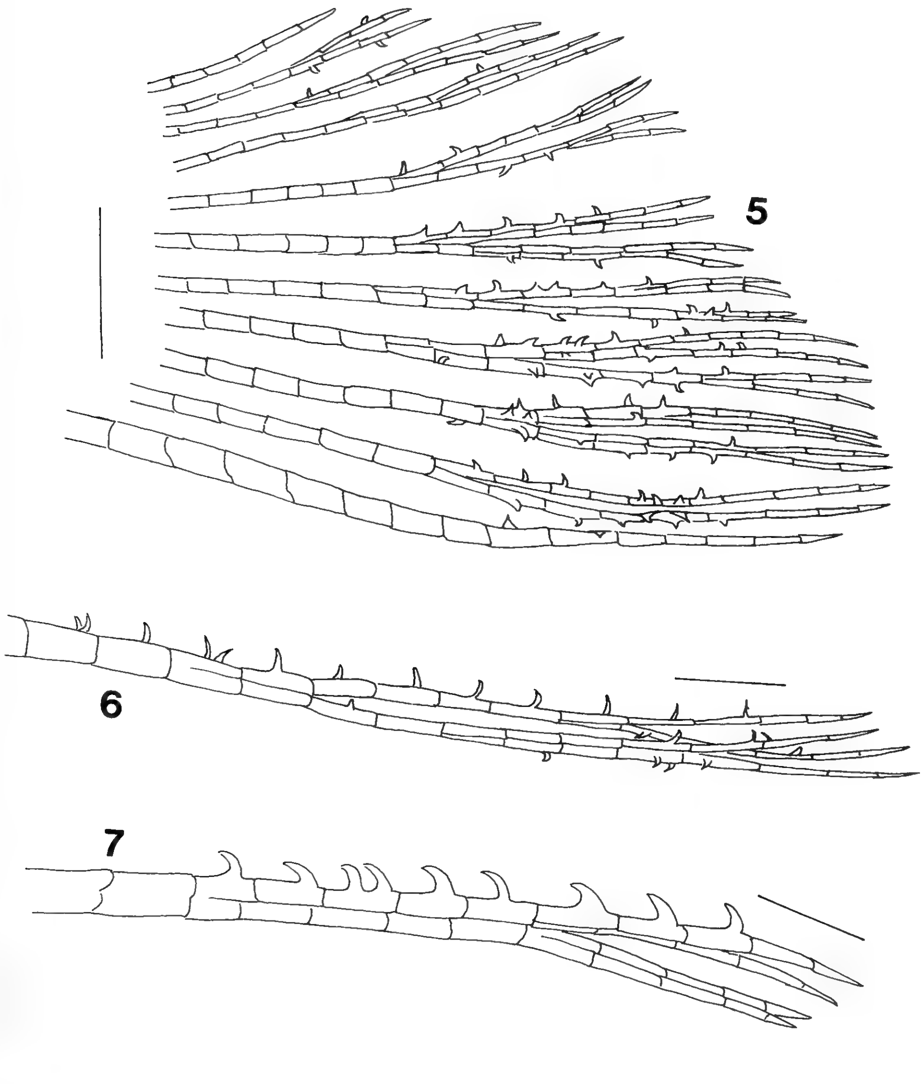
Dark chromatophores on distal margin of anal fin, forming a band; two or three first dorsal rays with black chromatophores; middle caudal-fin rays black, also tips of caudal-fin rays with dark chromatophores; pectoral and pelvic fins hyaline.

ETYMOLOGY

The specific epithet is the name of a spirit, protector of the fresh waters, in the tupí-guaraní language.

DISCUSSION

Eigenmann (1921, 1927) separated the species of the genus *Astyanax* into three subgenera that were maintained by many authors. *Astyanax ojiara* has low body depth and a complete series of scales in the predorsal area. Following Géry (1977), *A. ojiara* is placed in the group with 32-41 scales in the lateral line. Among those species, the number of anal-fin rays of *A. ojiara* agrees with that of *A. fasciatus* group. Like Géry (1977) pointed out, the other group is defined by the presence of 17-24 anal-fin rays,



FIGS 5-7

Astyanax ojiara, dorsal view, SL 45.0 mm. 5: left pectoral fin, scale= 1 mm; 6: detail of hooks on second branched pelvic-fin ray, scale= 0.5 mm. 7: *A. eigenmanniorum*, dorsal view, SL 45.0 mm, detail of the same ray, scale= 0.5 mm.

except *A. eigenmanniorum*. The number of perforated scales in the lateral line and the number of anal-fin rays of *A. ojiara* ressemble those of *A. eigenmanniorum*. Nonetheless, the number and shape of teeth greatly differ. *Astyanax eigenmanniorum* has 4-5 teeth in the outer series of premaxilla and 5 teeth in the inner one, with the central cusp notably larger; the maxillary tooth has 3 to 5 cusps (Azpelicueta, 1979); all those teeth always have broad bases. The dentary bears 4 large teeth, a median one, and a series with 5 to 7 very small teeth. In comparison, the maxilla of *A. eigenmanniorum* is narrow and long, always reaching the anterior third of the eye; the premaxilla has a longer dorsal process. *Astyanax eigenmanniorum*, as described by Cope (1876), has pectoral fins that reach ventral-fin origin, a character always present in the Brazilian specimens examined; the length of pelvic fins and the preanal distance have similar values that those of males of *A. ojiara*. The pelvic-fin hooks of *A. eigenmanniorum* are strong and regularly placed (Figs 6, 7); the anal-fin hooks develop on the first ten rays whereas they are smaller, more numerous and are present on many anal-fin rays of *A. ojiara*. In *A. eigenmanniorum*, the eye, the postorbital length, and the interorbital distance are larger.

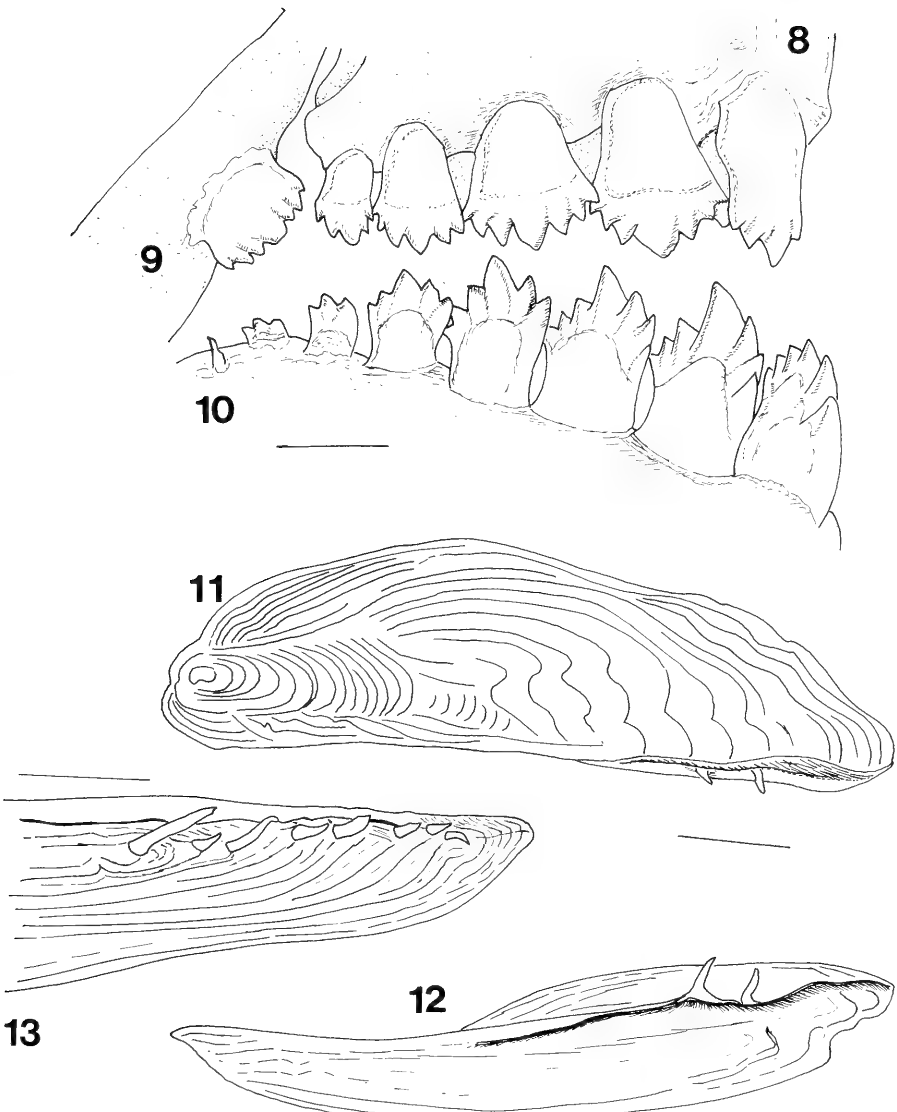
From other species of the *A. eigenmanniorum* group, *A. ojiara* is distinguished by one maxillary heptacuspid tooth, and the hooks developed in all fins of males. *Astyanax taeniatus* (Jenyns, 1842) and *A. giton* Eigenmann, 1908 have dentary teeth decreasing in size anteroposteriorly. Lucena & Lucena (1992) discussed the presence of that feature as a character that evolved in different species of the genera *Deuterodon* and *Astyanax*.

Different measurement relations in both sexes of *A. ojiara* are the length of pelvic fin, the distances between last branched anal-fin ray-hypural joint, snout tip-anal-fin origin, and origins of pelvic and anal fins (Table 1). Two thirds of the sample examined were males.

Presence of hooks in Characidae

Sexual dimorphism appears in many characids; hooks develop in different fins of males, excluding the genus *Cheirodon* in which female pelvic fins bear hooks (Malabarba, 1998, fig. 16). One of the attributes of secondary sexual characteristics is its appearance during breeding season, followed by regression. Nonetheless, the specimens of *A. ojiara* examined were collected in May -the end of fall in southern hemisphere-, and neither males nor females were mature. Therefore, hooks are always present in the new species; this fact has been observed in the genera *Cheirodon* and *Hyphessobrycon* as well.

In several subfamilies of Characidae such as Iguanodectinae, Stethaprioninae, Glandulocaudinae or Cheirodontinae and in different lineages within the family, males usually show hooks on anal and pelvic fins, but sometimes they occur on caudal or dorsal fins. Within the Cheirodontinae, some species as *Serrapinus calliurus* bears hooks in anal fin while many other ones have hooks on anal and pelvic fins. Among them, *C. pisciculus*, *C. terrabae*, *C. dialepturus*, *C. affinis*, *C. gorgonae* (Fink & Weitzman, 1974), *C. ortegai* (Vari & Géry, 1980), and *C. interruptus* (pers. obs.), *Serrapinus kriegi* and *S. microdon* (Uj, 1987; pers. obs.); and *Heterocheirodon yatay*



FIGS 8-13

FIGS 8-10: *Astyanax ojiara*, lingual view of left teeth, SL 48.0 mm, scale= 0.5 mm. 8: inner row of premaxillary teeth, with tips gently expanded distally; 9: maxillary tooth with seven small cusps; 10: eight dentary teeth, decreasing in size anteroposteriorly. FIGS 11-13. *Astyanax ojiara*, left pectoral axillary scale of males, SL 42.0 mm; 11: lateroventral view, scale= 0.5 mm; 12: profile of the same scale; 13: inner view, detail of one cleared and stained specimen with 8 hooks, SL 56.0 mm, scale= 0.5 mm.

(Casciotta *et al.*, 1992). Hooks are not common in the caudal fin, but, Fink & Weitzman (1974) described and illustrated hooks not only on the caudal fin of *Saccoderma hastata* but also on that fin of *Cheirodon dialepturus*.

In glandulocaudine species, with notable sexual dimorphism, hooks may occur on caudal fin, as in *Xenurobrycon macropus* (Mahnert & Géry, 1984; Weitzman & Fink, 1985), *X. pteropus*, *Scophaerocharax octopodus*, *Corynopoma risei*, *Gephyrocharax atricaudatus* (Weitzman & Fink, 1985), *Mimagoniates microlepis* and *M. reocharis* (Menezes & Weitzman, 1990), *Ptychocharax rhyacophila* (Weitzman *et al.*, 1994) *Tyttocharax cochui* (Weitzman & Ortega, 1995). The presence of hooks in anal and pelvic fins is usual among glandulocuadine fishes; the position, size and shape of the hooks vary in different species. Mahnert & Géry (1984) mentioned the occurrence of hooks on the pectoral fin only in one specimen of *X. macropus*.

Many other species of characins have been described with hooks; some of them have hooks on anal fins as *Hyphessobrycon diancistrus* (Weitzman, 1977a) and *H. procerus* (Mahnert & Géry, 1987) or hooks may be present on pelvic fins as in *Paracheirodon axelrodi* (Weitzman & Fink, 1983). In most of the species, hooks develop on anal and pelvic fins: *Hyphessobrycon guarani* (Mahnert & Géry, 1987), *H. arianne* (Uj & Géry, 1989), *H. epicharis* (Weitzman & Palmer, 1997), *H. wajat* (Almirón & Casciotta, 1999), *Rachoviscus gracilipes* and *R. crassipes* (Weitzman & Gonçalves da Cruz, 1981), *Piabarcus annalis* and *P. torrenticola*, *Creagrutus paraguayensis* (Mahnert & Géry, 1988), some Trans-Andean species of *Creagrutus* as *C. caucanus*, *C. maracaiboensis*, *C. paralacus* or *C. affinis* (Harold & Vari, 1994), *Hemigrammus mahnerti* (Uj & Géry, 1989), *Bryconamericus iheringi* (pers. obs.).

Well developed hooks occur also on anal or pelvic fins of other characiform species such as *Brycon microlepis* (Géry & Mahnert, 1992), the miniature *Priocharax ariel* (Weitzman & Vari, 1987), *Toracocharax stellatus* (pers. obs.) as well as in some species of different genera of the Stethaprioninae such as *Poptella*, *Stethaprion*, *Brachychalcinus* and *Orthospinus* (Reis, 1989).

In the genus *Jupiaba*, *J. meunieri* or *J. maroniensis* (Gery *et al.*, 1996, as *Astyanax*) show hooks on the anal fin. Within *Astyanax*, hooks on anal and pelvic fins have been reported in *Astyanax maculisquamis* (Garutti & Britski, 1997), *A. alburnus* (Malabarba, 1983 as *A. hasemani*), *A. kullanderi* (Costa, 1995), *A. unitaeniatus* (Garutti, 1998), *A. eigenmanniorum*, *A.* cf. *fasciatus*, *A.* cf. *asuncionensis* or *A. alleni* (pers. obs.). None of those species have caudal fin hooks.

Extremely scarce is the information about the presence of hooks on dorsal fin; Weitzman (1977b) found hooks on that fin in two species of *Hyphessobrycon* only, the Amazonian *H. socolofi* and *H. erythrostigma* which bears very few hooks.

The hooks of the pelvic axillary scale appear in medium sized males of *A. ojiara* and their number varies in different specimens, although one or two hooks are present usually (Figs 11, 12). One cleared and stained specimen has eight hooks (Fig. 13) on that scale. No other characids have been described with hooks on all fins or on pelvic axillary scale.

TABLE 1

Morphometrics of holotype, 12 females and 12 males (paratypes) of *Astyanax ojiara*. Minimum, maximum and mean in parenthesis. DLAR-HJ= distance between last anal-fin ray and hypural joint.

	Holotype	females	males
Standard length	50.5	39.8-72.0	38.0-53.5
% of standard length			
Predorsal distance	51.4	51.8-56.9 (44.8)	50.5-53.1 (51.3)
Preventral distance	49.3	48.7-51.6 (50.4)	47.7-51.3 (48.8)
Preanal distance	64.0	65.8-70.4 (67.7)	61.3-65.9 (63.4)
Body depth	35.0	35.5-40.0 (38.1)	34.0-37.9 (36.5)
Dorsal-fin base	13.4	13.8-17.2 (15.4)	12.8-15.9 (13.3)
Anal-fin base	32.4	27.6-33.4 (30.5)	30.0-34.6 (32.2)
Pectoral-fin length	23.3	20.3-24.6 (21.7)	22.1-24.5 (23.2)
Pelvic-fin length	19.6	14.8-18.3 (16.5)	17.9-21.5 (19.0)
Distance between pectoral and pelvic fin origins	22.5	20.4-25.7 (23.2)	21.8-24.6 (23.4)
Distance between pelvic and anal fin origins	19.2	19.6-22.8 (21.3)	16.1-20.0 (18.2)
Head length	27.7	27.3-29.5 (28.1)	26.5-29.7 (27.8)
% of DLAR-HJ			
Peduncle depth	90.7	90.0-110.0 (99.0)	74.6-90.7 (83.0)
% of head length			
DLAR-HJ	46.4	38.8-46.4 (42.3)	46.8-56.8 (50.2)
Snout length	28.5	24.5-30.9 (27.7)	27.8-30.5 (29.2)
Eye	35.7	29.1-37.2 (28.1)	32.3-35.9 (34.3)
Postorbital length	57.1	50.0-54.8 (52.4)	53.4-57.2 (55.8)
Interorbital length	32.8	31.0-34.6 (33.0)	31.0-35.6 (32.5)
Maxillary length	22.8	21.1-24.5 (22.8)	37.1-40.6 (38.8)

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Revision of the genus *Ebbrittoniella* Martínez (Coleoptera: Scarabaeoidea: Ceratocanthidae)[1]

Alberto BALLERIO
Viale Venezia 45, I-25123 Brescia, Italy.
E-mail: ballerio@numerica.it

Revision of the genus *Ebbrittoniella* Martínez (Coleoptera: Scarabaeoidea: Ceratocanthidae). - The Oriental genus *Ebbrittoniella* Martínez, 1962 is redescribed. The current spelling *Eubrittoniella* is emended. *Cyphopisthes gestroi* (Paulian, 1942) is transferred to *Ebbrittoniella*. Presently the genus includes *E. ignita* (Westwood, 1883) and *E. gestroi* (Paulian, 1942). Some features of male and female genitalia and the affinities of the genus are briefly discussed.

Key-words: Coleoptera - Scarabaeoidea - Ceratocanthidae - *Ebbrittoniella* - Taxonomy - Oriental Region.

INTRODUCTION

In 1883 Westwood described *Acanthocerus* (*Sphaeromorphus*) *ignitus* on the basis of a specimen from Sumatra. In the subsequent fifty years Preudhomme de Borre (1886), Lansberge (1887), Gestro (1899) and Arrow (1912) dealt with this species; among these authors Gestro for the first time stressed the unnatural generic placement of the taxon, being the only Oriental representative in a New World genus. In 1962 Martínez, by examining a specimen from Sarawak in BMNH, followed Gestro's suggestion and created the new genus *Ebbrittoniella* to accommodate the taxon *ignitus*, while pointing out that the closest genus to it was the Neotropical genus *Acanthocerus* Macleay, 1819 (now *Ceratocanthus* White, 1842).

Paulian in his revision of Oriental Ceratocanthidae (1978) summarized available distributional data, redescribed the species and placed it in the key near *Cyphopisthes* Gestro, 1899. He also emended the name in *Eubrittoniella ignitus*. This emendation cannot be considered justified according to the art. 33 of ICZN, because in the original paper there is no clear evidence of an author's lapsus calami or printer's error as defined by art. 32 of ICZN and therefore the original spelling *Ebbrittoniella* should be maintained.

After that point the genus *Ebbrittoniella* has been listed only by Browne & Scholtz (1995, 1996, 1998) as *Eubrittoniella*, in a series of papers upon the hindwing articulation, base and venation of the Scarabaeoidea.

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[1] 5th contribution to the knowledge of Ceratocanthidae.

Manuscript accepted 28.02.2000

During revisionary studies on Old World Ceratocanthidae I had the opportunity to examine the type material as well as specimens from several collections, allowing me to confirm the validity of the genus. *Cyphopisthes gestroi* (Paulian, 1942) shares all the generic characters and therefore it is now transferred to *Ebbrittoniella*.

METHODS AND ACRONYMS

Elytral length is measured from the apex of elytral articular process to the more external point of the apical convexity, total width measurements are the sum of both elytral widths.

Drawings of genitalia were taken from pieces previously cleaned with 10% KOH solution.

Terminology follows Nel & De Villiers (1988) and Nel & Scholtz (1990) for mouthparts, Kukalová-Peck & Lawrence (1993) for wing venation and D'Hotman & Scholtz (1990) for male genitalia (thus the dorsal side of aedeagus is the concave one); for the remaining conventions I refer to Ballerio (2000).

EL	maximum elytral length
EW	maximum total elytral width
HL	maximum head length
HW	maximum head width
L	length
PL	maximum pronotum length
PW	maximum pronotum width
W	width
ABCB	A. Ballerio private collection, Brescia (Italy)
BMNH	The Natural History Museum, London
BPBM	Bernice Bishop Museum, Honolulu
HNHM	Hungarian Natural History Museum, Budapest
MCSN	Museo Civico di Storia Naturale "Giacomo Doria", Genova
MHNG	Muséum d'histoire naturelle, Genève
MNHN	Musée national d'Histoire naturelle, Paris
NHMW	Naturhistorisches Museum, Wien
NMPC	National Museum (Natural History), Praha
OXUM	Hope Department of Entomology, Oxford University, Oxford
RMNH	Nationaal Natuurhistorisch Museum, Leiden
SACF	S. Adebratt private collection, Frinnaryd/Boxholm (Sweden)
SMTD	Staatliches Museum für Tierkunde, Dresden
ZMUC	Zoologisk Museum, Københavns Universitet, København

TAXONOMY

Ebbrittoniella Martínez

Ebbrittoniella Martínez, 1962: 61 (description)
Eubrittoniella Martínez, Paulian, 1978: 506 (emendation)

Type species: *Acanthocerus (Sphaeromorphus) ignitus* Westwood, 1883 by original monotypy.

Etymology: named after Dr. E. B. Britton, former curator at BMNH. The gender is feminine.

DIAGNOSIS

The genus can be identified by the following combination of characters: labrum distally abruptly truncate, truncature marked dorsally by a slight carina bearing a row of long, erect, fine setae, truncature in frontal view forming a plate irregularly semicircular, with semicircumference corresponding to the carina; genal canthus complete, touching the occipital area; dorsal ocular area large; anterior angles of pronotum broadly rounded; mesotibiae short and wide (W/L ratio = 0.3), in ♂♂ with the inner apical spur straight and very short; protibiae with outer edge almost smooth (low magnification), ending with a single tooth in both sexes; apical spur of protibiae sharp and slender.

DESCRIPTION

Medium to large Ceratocanthidae; volant.

Head: W/L ratio = 1.8, subpentagonal, anterior edge forming a triangle with obtuse apex (about 150°), both sides of the triangle smooth and almost rectilinear, not reflexed upward; genae aligned with fore edge, forming a right angle with genal canthus; genal canthus narrow, straight and complete, touching the occipital area; dorsal ocular area large; dorsal interocular area about five times the maximum width of the dorsal ocular area; ventral ocular area very large; head surface almost plane.

Pronotum: W/L ratio = 1.8, slightly wider than maximum elytral width, evenly and broadly convex; anterior edge feebly bisinuate; anterior angles distinctly but slightly protrudent forward, broadly and regularly rounded; sides obtusely rounded; base narrow, a very thin bead present anteriorly and at each side of base; base with a weak callosity marking each extremity of base of scutellum.

Scutellum: very large, longer than wide (W/L ratio = 0.7), sides proximally subparallel and distinctly notched by apical portion of mesepisternum and elytral articular process, then convergent to form a triangle with apex very elongate and acute and sides slightly curved inward; apical portion of mesepisterna (see Ballerio, 2000) visible from above, very large, larger than elytral articular process, subrectangular, smooth and shiny (Fig. 2d).

Elytra: slightly longer than wide (W/L ratio = 0.9), maximum width near middle, apex in lateral view fairly reentering inward; slightly flattened on disc, then abruptly convex at sides to form a pseudoepipleuron not marked by any lateral carina; marginal elytral area narrow, almost indistinct; elytral suture very feebly raised; sutural stria very fine and close to suture, limited to distal third; inferior sutural stria absent; striated articular area well developed and visible in lateral view, relatively wide and long; elytral articular process well developed, smooth and shiny.

Apical extremity of clypeus (see Ballerio, 2000) short and transversely grooved. Labrum (Fig. 4b) wide and short, proximally with surface microreticulated, distally

abruptly truncate, truncature marked dorsally by a slight carina bearing a row of long, erect, distally curled, fine setae; truncature in frontal view forming a plate irregularly semicircular, with semicircumference corresponding to the carina; surface of plate almost smooth, bearing few long setae. Distal epipharynx longitudinally divided by a very sharp strong anterior median process, distally very raised; median brush and corypha absent; apical fringe made of long fine setae, absent in the middle; lateral combs made of long fine setae. Mentum ventrally flat, deeply emarginated in the middle of anterior edge, emargination regularly wide-U-shaped; labial palpi (including palpiger) four jointed, first joint short and transverse, joint two securiform, joint three short and ovoidal, the same length of the second, and joint four subconical, about two times the length of the former, all joints, apart from the last one, fringed with long setae. Maxillae (Fig. 3a) with a very elongate single lacinia, covered with fine long setae, monolobed galea proximally sclerotized and distally clothed with very coarse short thick bi- or triphid setae (galeal brush) (Fig. 3b); maxillary palpi (including palpiger) four jointed, palpiger very small, joint two wide and relatively short, distinctly wider than the following joints, joint three about as wide as long, joint four long and subconical, slightly longer than the preceding two together, apically bearing some short sensilla. Mandibles elongate, slightly asymmetrical, apicalis more or less gently bent at about a right angle with apex short and acutely pointed, mesal brush narrow and well developed, conjunctive present, molar lobe very strong. Antennae 10-jointed, scape large, distally subcarinate (securiform), distally bearing some setae, funicle short with pedicellum plump and rounded, the remaining joints very short, distinctly wider than long, antennal club three-jointed, joints hairy, relatively short, narrow; club small, about as long as wide and as wide as the length of funicle (L funicle/L lamellae ratio = 2.1).

Ventral areas of prothorax: (Fig. 4a) sides of propleura smooth, very excavated and folded in, excavation with a further shallow narrow reniform excavation inside (visible also in dorsal view against the light as a dark reniform patch). Procoxae transversely oriented, apices nearly touching each other. Anterior trochanters with anterior tips bearing a tuft of long setae. Profemora slender (W/L ratio = 0.2), posterior edge without emargination, surface smooth. Protibiae almost straight, outer edge smooth at low magnfication (at most very slightly serrate: few feeble denticles visible at 45x); apical spur relatively short, sharp, very gently and feebly curved downward. Protarsi with first article as long as the following three together, articles two and three slightly dilated, article five slightly longer than the former; each tarsomere, with the exception of the last one, ventrally bearing a tuft of dense fine setae. Mesosternum forming a sharp fine carina, protruding between mesocoxae and joining metasternum. Mesocoxae almost adjacent to each other, longitudinally oriented. Trochanters with acute posterior tip. Mesofemora slender (W/L ratio = 0.3), surface smooth, with posterior edge emarginated at distal third, emargination preceded by a small distinct tooth. Mesotibiae subrectangular, short (W/L ratio = 0.3), inner angle of apex with two straight apical spurs. Mesotarsi inserted near the inner angle of apical edge, slightly longer than apical edge of tibia (exceding it for the length of the last tarsomere), with first three articles subequal in length, fourth shorter, fifth almost as long as the preceding two; each tarsomere, with the exception of the last one, ventrally bearing a

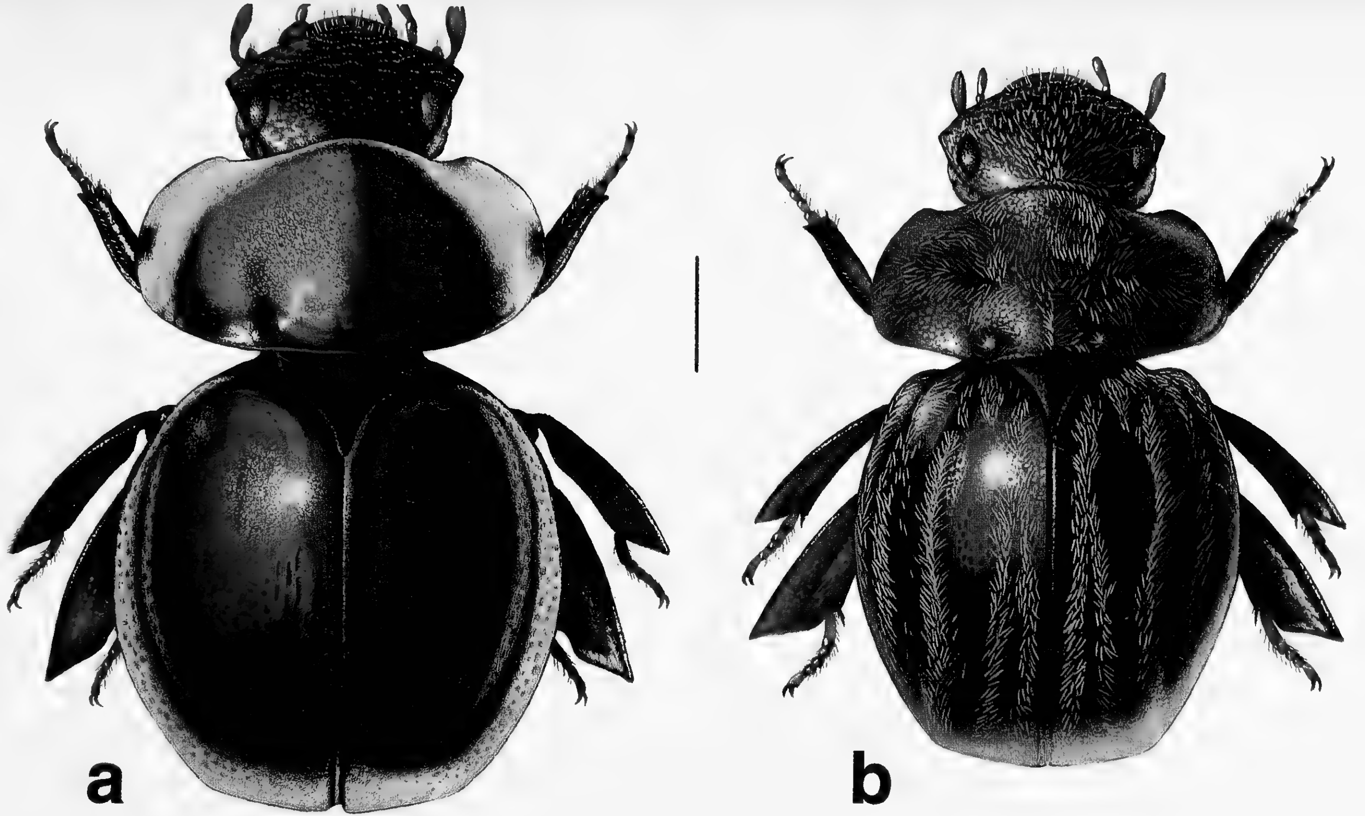

FIG. 1 – a: *Ebbrittoniella ignita* (Westwood), habitus of adult (Lata Jarom); b: *Ebbrittoniella gestroi* (Paulian), habitus of adult (Cameron Highlands) (drawings by J. Kobylák) (scale bar: 1mm).

tuft of dense setae. Trochanters of metafemora with acute posterior tip, metafemora plumper than mesofemora (W/L ratio = 0.3), surface wrinkled, posterior edge distally with a small emargination. Metatibiae triangular, wide (W/L ratio = 0.5), ending with two straight sharp fine paired spurs. Metatarsi almost as long as the apical edge of tibia, first article almost as long as the following three together, fifth almost as long as the first one; each tarsomere, with the exception of the last one, ventrally bearing a tuft of dense setae.

Wings (Fig. 2a) (Lwing/Lelytron ratio = 2.1): fully developed, MP_{1+2} - RP loop present with RP long (although weakly sclerotized), MP_4 medium sized, apical field with a vertical secondary sclerification near the radial cell. First axillary with no appreciable differences at species level (Fig. 2b).

Sexual dimorphism: ♀♀ (Fig. 2c: B) have the apical outer tooth of protibiae distinctly sharper and more protruding outward and forward than in ♂♂ (Fig. 2c: A) and mesotibiae with the inner apical spur straight and approximately as long as the outer, while in ♂♂ it is straight but very short and very difficult to detect.

Male genitalia: Genital segment (Fig. 5c) Y-shaped (no appreciable differences at species level), fairly sclerotized, with a distinct manubrium about as long as the basal triangle, branches forming the manubrium apparently not fused together, although connected by a transparent membrane (after treatment with KOH), base of triangle very weakly sclerotized; basal piece of aedeagus large and twisted (Fig. 5a), about four times the length of parameres; internal sac very large about three times as long as tegmen, internal sac distally with coarse spicules and setae; temones present; parameres (Fig. 5b) short and slightly asymmetrical (hardly appreciable differences at species level), laterally flattened, between parameres dorsally lies a narrow subtriangular sclerite.

Female genitalia: bursa copulatrix (Fig. 5d) with one small symmetrical subcircular or subtriangular sclerite (very variable in shape and without appreciable differences at species level) with a hole in the middle; spermatheca (Fig. 6) strongly sclerotized, large and distinctly wide-U-shaped; genital palpi weakly sclerotized, subcircular, relatively small and short.

Ebbrittoniella ignita (Westwood, 1883) Fig. 1a

Acanthocerus (Sphaeromorphus) ignitus Westwood, 1883: 2 (description)
Acanthocerus (Sphaeromorphus) ignitus Westwood: Preudhomme de Borre, 1886: 80 (catalogue)
Synarmostes ignitus (Westwood): Lansberge, 1887: 209 (list)
Acanthocerus ignitus Westwood: Gestro, 1899: 462 (redescription, distribution and key)
Acanthocerus ignitus Westwood: Arrow, 1912: 49 (catalogue)
Ebbrittoniella ignita (Westwood): Martínez, 1962: 61 (redescription and iconography)
Eubrittoniella ignitus (Westwood): Paulian, 1978: 506 (redescription, distribution, iconography and key)

Type locality: Koetoer (Indonesia: Sumatra).

Material examined - Holotypus ♂: Koetoer 6.78 / Sum. Exp. Koetoer 6.78 / Typus / *Acanthocerus ignitus* Westw. / Museum Leiden *Acanthocerus ignitus* det. Westwood / 6903 / *Eubrittoniella ignitus* (Westw.) R. Paulian det. / *Ebbrittoniella ignita* (Westw.) A. Ballerio det. 1997 (RMNH), [very damaged specimen, pinned, lacking the head, which is glued together with legs and mouthparts on a card pinned with a separate pin, without any data bearing label].

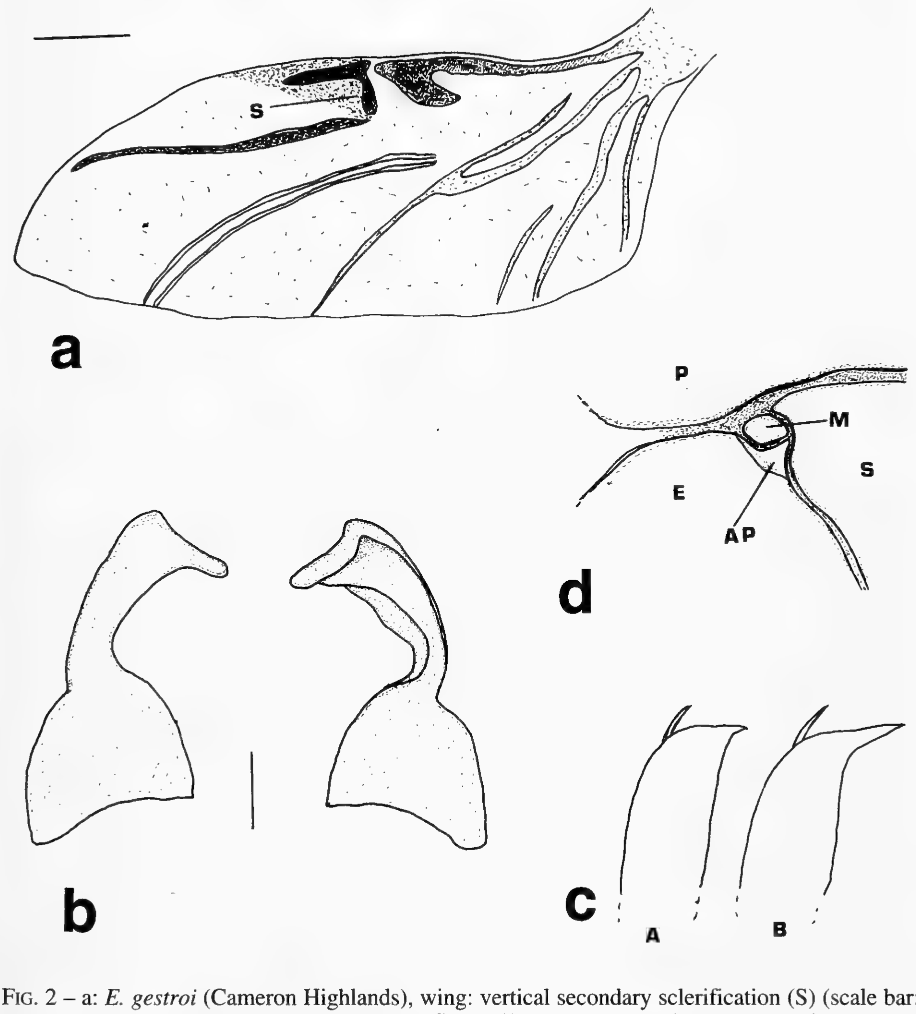

FIG. 2 – a: *E. gestroi* (Cameron Highlands), wing: vertical secondary sclerification (S) (scale bar: 1 mm); b: *E. gestroi* (Cameron Highlands), first axillary (scale bar: 0,1 mm; c: *Ebbrittoniella*, apex of foretibiae (dorsal view): (A) male, (B) female; d: *Ebbrittoniella*, area near scutellum as seen when the beetle assumes the "rolled up" posture: apical portion of mesepistemum (M), articular process of elytron (AP), scutellum (S), elytron (E), pronotum (P).

Other 32 specimens (7 ♂♂ and 4 ♀♀ dissected). INDONESIA. Kajoe Tanam [Sumatra], Klein (ZMUC); Sumatra, Manna, M. Knapper (RMNH); Ruuyer Payakor, Sumatra (RMNH); Sentinjak, Sumatra, 1800 ft., Jan. '98, 99-95 (BMNH); Setinjak, W. Sumatra, I to VII. 98, (Ericsson) (Coll. C. Felsche, Kauf 20, 1918) (SMTD); Sumatra, Padang Sidempoean, XII.1902-I.1903 (MNHM); Sumatra (ex Mus. Van Lansberge) (MNHM). Nias Island. Is. Nias, U. Raap (MNHM); Hili Madjedja, N. Nias, 4me trim. í95, I.Z. Kannegieter (ex Mus. Van de Poll) (MNHM); Is. Nias 1897-98, U. Raap (RMNH); Is. Nias 1897-98 U. Raap (MCSN). Kalimantan-Timur: Apokayan, Long Sungei Barang 900 m, secondary forest, 15-23.02.1997, leg. C. & P. Zorn. MALAYSIA. Malay penin.: Selangor, Giunting Simpak, Jan. 2nd 1933, N.M. Pendlebury,

F.M.S. Museum (BMNH); Malaysia: Pahang/Johor, Endau Rompin NP, 100 m, Salendang, 28.2-12.3 1995, leg. Strba & Hergovits (NHMW); Malaysia – Pahang, Banjaran Benom, Lata Jarom, 6-8.3.1997, Ivo Jeniš leg. (ABCB); ibidem, 18-21.3.1997, Ivo Jeniš leg. (ABCB), W. Malaysia, Pahang, Baniaran Benom Mts., K. Ulu Dong 10-15 km SSE, 17-23.IV.1997, D. Hauck leg. (ABCB); Sarawak, C. S. Brooks, B.M. 1928-193 (BMNH); Malaysia: Sabah, Sipitang, Mendolong, T1B/W4, 11.V.1988, leg. S. Adebratt, 12-60, 2859BC (SACF). OTHER. Sunda-Inseln v. Studt /coll. Petrovitz (MHNG).

DESCRIPTION

HL= 0.8-1.2 mm HW= 1.6-2 mm PL= 1.5-2 mm PW=2.8-3.3 mm EL= 2.9-3.9 mm EW= 2.7-3.6 mm.

Dorsally very shiny and entirely brightly metallic: red with gold/green faint, elytral suture, scutellum, sides of elytra, sides of pronotum and sides of head deep electric blue with green faint; ventrally alutaceous, reddish brown, antennae yellowish. Pubescence invisible at low magnification, otherwise formed by very short and fine hyaline erect setae, subject to wear. Head surface with a variable number of transverse lines, occupying anteriorly the two thirds of head; vertex with sparse simple punctures, often preceded by a very short transversal impressed line. Pronotum very convex, surface with very small horseshoe-shaped punctures (containing a small simple puncture in the middle) or sometimes simple punctures, never very dense, usually sparser on disc and slightly coarser near anterior angles; the horseshoe is opened outwards in the punctures at sides and inwards in the punctures on the disc. Scutellum with horseshoe-shaped punctures with horseshoe opened toward apex, punctures denser near sides. Elytra distinctly convex, surface with punctures horseshoe-shaped, small, never very dense, variably distributed, horseshoe opened toward suture or apex; two longitudinal lines along the suture at medial and distal third of length; pseudoepipleura with some longitudinal lines; humeral callus not protruding; articular area very large. Outer face of meso- and metatibiae with short impressed lines varying from longitudinal to transverse and short erect setae through the entire surface. Wings with vertical secondary sclerification of apical field finer than in *E. gestroi* and MP_{1+2} - RP loop shorter. Spermatheca as in figs. 6a, b, c, d.

VARIABILITY

Although the majority of individuals examined shows the typical colours, one pair from Pahang is uniformly dark green, one individual from Nias is uniformly deep amaranth and the individual from Sabah is yellowish with greenish metallic sheen; there is a strong variability also in the punctures (mostly the ones of pronotum), which vary in size and density: the specimen from Sabah has the entire head surface covered by transverse lines, the amaranth specimen from Nias has the entire pronotum completely smooth, while the pair of dark green specimens has punctures coarser and more impressed than the other specimens. The very fine pubescence varies and in some specimens is no longer visible (probably ripped off by wear).

DISTRIBUTION AND HABITAT

Recorded from Peninsular Malaysia, Sumatra, Nias Island and Borneo. For habitat see under *E. gestroi*.

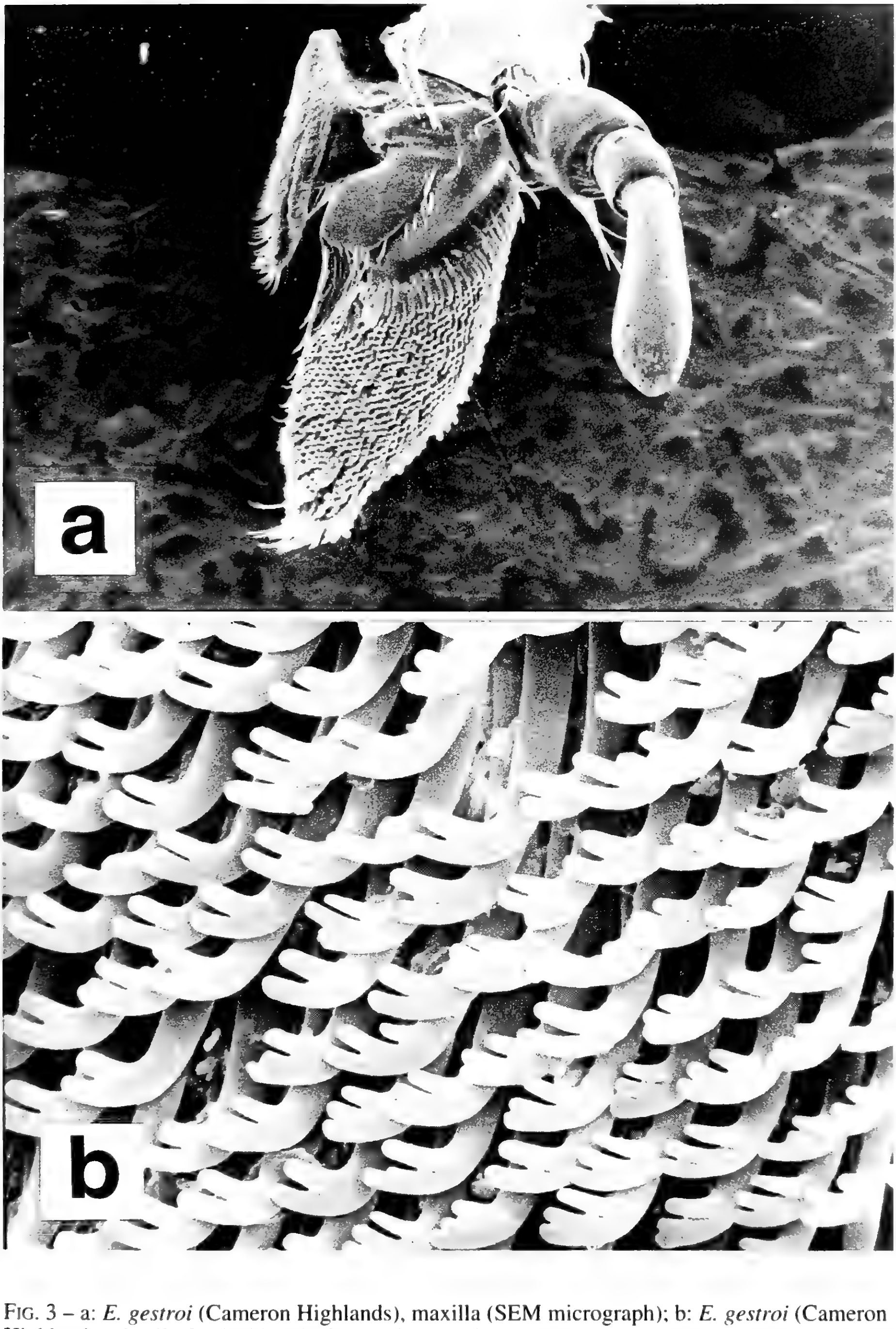

FIG. 3 – a: *E. gestroi* (Cameron Highlands), maxilla (SEM micrograph); b: *E. gestroi* (Cameron Highlands), detail of galeal brush (SEM micrograph).

REMARKS

Westwood (1883) described also a variety "paullo minor, obscurior,..." from Sarawak without naming it; examination of the specimen in OXUM revealed that it is an *Eusphaeropeltis* sp.

Ebbrittoniella gestroi (Paulian, 1942) comb. n. Fig. 1b

Philharmostes Gestroi Paulian, 1942: 70 (description and key)
Cyphopisthes gestroi (Paulian): Paulian, 1978: 512 (new combination, redescription, distribution, iconography and key)

Type locality: Palembang (Indonesia: Sumatra).

Etymology: named after Dr. R. Gestro, late director of MCSN and specialist of Ceratocanthidae.

Material examined – Holotypus, ♀: Sumatra Palembang / Type / *Cyphopisthes gestroi* n. sp. det. R. Paulian, 1937/ *Ebbrittoniella gestroi* (Paulian) n. comb. det. A. Ballerio, 1997. (MNHN) [completely rolled up and glued on a card] .

Other 141 specimens (15 ♂♂ and 15 ♀♀ dissected) – INDONESIA. Palembang [Sumatra], 1900, Bouchard (MCSN); MALAYSIA. Malaya: (W) Perak, Maxwell Hill, 1350 m., 17-20.III.1958, T.C.Maa collector, Bishop (BPBM); Malaysia – Perak, Banjaran Bintang, Maxwell Hill (Taiping), 18-19.2.1997, leg. Ivo Jeniš (ABCB); West Malaysia, Perak, Maxwell Hill, 900-1000 m, above Taiping City, 12-16.1.1995, leg. S. Bečvar j. & s. (ABCB); W. Malaysia, Perak: 25 km NE of Ipoh, 2100 m, Banjaran Titi Wangsa mts., Gunung Korbu, 4-13.III.1998, P. Čechovský leg.; W. Malaysia, Perak, 25 km NE of Ipoh, 1200 m, Banjaran Titi Wangsa mts., Gunung Korbu, 27.I-2.II.1999, P. Čechovský leg.; W. Malaysia, Pahang, 30 km E of Ipoh, 1500 m, Cameron Highlands, Tanah Rata, 20.II-3.III. 1998, P. Čechovský leg.; ibidem, 22-26.I.1999, P. Čechovský leg.; P. Malaysia-Pahang: Cameron Highlands, Tanah Rata umg., gn. Jasar, 1300 m, 25.II.1997, leg. Schuh & Lang (ABCB); West Malaysia, Pahang, C. Highlands, Tanah rata, 20-25.1.1995, Gn. Jasar, 14-1500 m, leg. S. Bečvar j. & s. (ABCB); West Malaysia, Pahang, Cameron Highlands, Brinchang, 18-19.1.1995, Gunung Berembam, 1600 m, leg. S. Bečvar j. & s. (ABCB); Malaysia, Pahang, Cameron Highlands, 2 km S of Tanah Rata on Tapah Road, montane rainforest, at light no. 93, 29.III.1995, leg. O. Merkl & L. Szikossy (HNHM); Malaysia, Pahang, Cameron Highlands, Tanah Rata, from illuminated white washed walls no. 77, 23-31.III.1995, l. O. Merkl (HNHM); Malaysia – Pahang, Banjaram Benom, Lata Jarom, 6-8.3.1997, leg. Ivo Jeniš (ABCB); Malaysia – Perak, Cameron Highlands, Tanah Rata, 13-16.3.1997, leg. Ivo Jeniš (ABCB); Borneo (Brit. N.), Sandakan bay (SW), Sapagaya Lumber Camp, 2-20 m, XI-3-í57, J.L. Gressit Collector (BPBM); North Borneo (SE), Forest Camp,.19 km N. of Kalabakan, 18.XI.1962, Y. Hirashima, Light trap, Bishop (BPBM); ibidem, 7-10.XI.1962 (BPBM); ibidem, 27.X.1962 (BPBM); ibidem, 10.X.1962 (BPBM); Malaysia – Sabah, Crocker Range National park, Longkogungan env., Ca. 750-850 m a.s.l., 19-21.VI.1996, 7c (NHMW); Borneo: Sarawak Bau District, Bidi, 90-240 m. 3.IX.1958, T.C. Maa Collector Bishop (BPBM); Sarawak, Kapit dist., Sebong, Baleh riv., 9-21.3.1994, Sv. Bílý leg. (NMPC), Sarawak, Kapit dist., Rumah Ugap vill., Sut. Riv., 3-9.3.1994, Sv. Bílý leg. (NMPC); Sarawak: Gunung Mulu Nat. Park, R.G.S. Exped. 1977-8, J.D. Holloway et al. B.M. 1978-206, site 2, january, camp 4, Mulu, 1790 m, 452463, lower montane (moss) forest, acl-understorey (BMNH).

DESCRIPTION:

HL= 0.9-1.1 mm HW= 1.5-1.9 mm PL= 1.3-1.8 mm PW=2.7-3.2 mm EL= 3-3.5 mm EW= 2.7-3.2 mm.

Dorsally metallic bronze/green with reddish faint, head, pronotum, scutellum and elytra covered by long recumbent yellowish setae; ventrally alutaceous yellowish/ brown with antennae yellowish. Head as in *E. ignita* but completely covered by recumbent setae and dense punctures. Pronotum slightly less convex than in *E. ignita*,

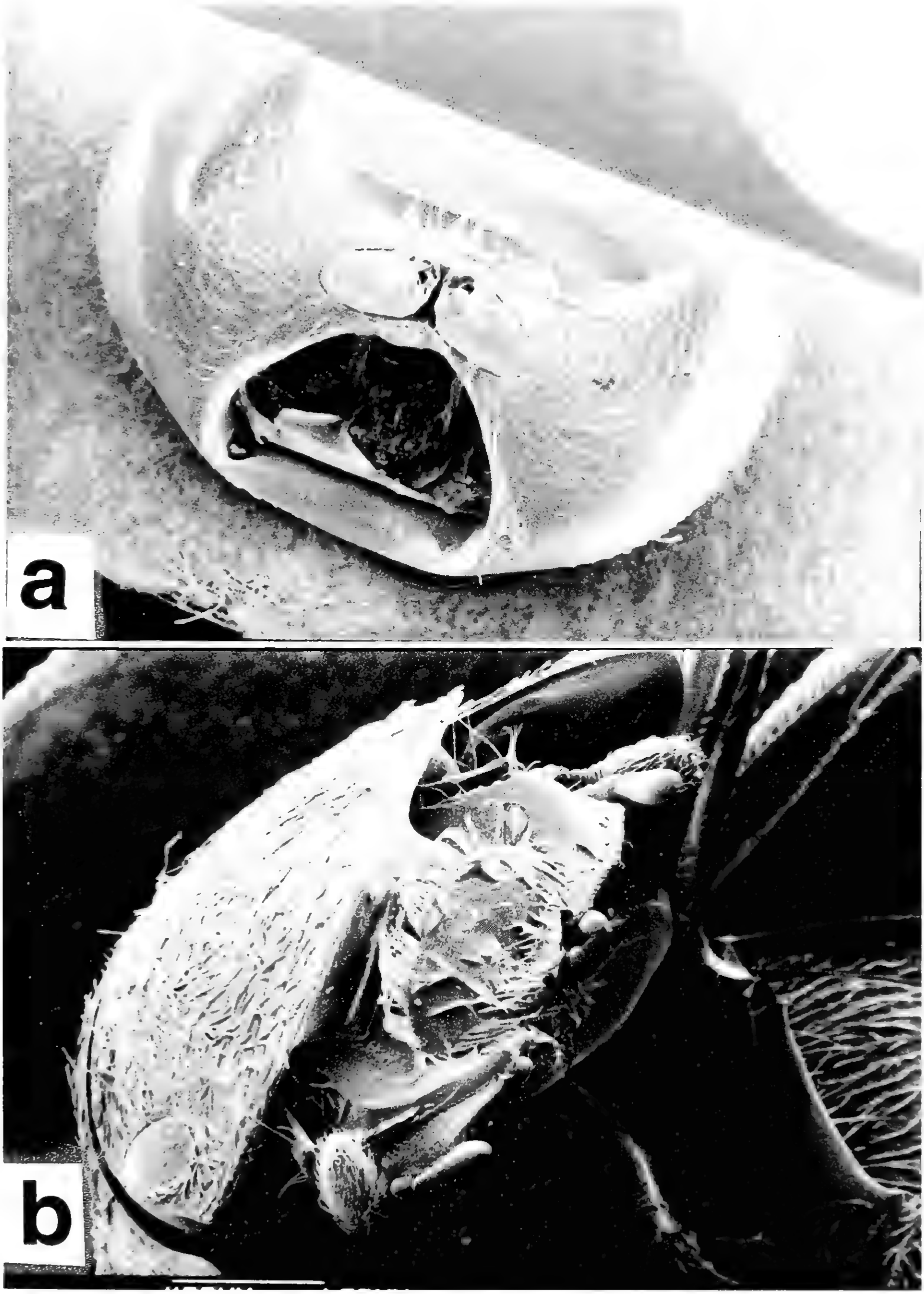

FIG. 4 – a: *E. gestroi* (Cameron Highlands): ventral areas of prothorax (SEM micrograph); b: *E. gestroi* (Cameron Highlands): head in fronto-lateral view, showing the truncature of labrum (SEM micrograph).

surface completely covered by very dense small horseshoe-shaped punctures, with horseshoe very short and almost transversal; each horseshoe with a small impressed puncture in the middle; pubescence very long and dense, recumbent, some subcircular small and weak depressions at each side of disc. Scutellum with coarse horseshoe-shaped punctures and long recumbent pubescence. Elytra slightly less convex than in *E. ignita*, surface with punctures less dense and slightly larger than on pronotum, relatively sparser near suture; proximal third with large longitudinal smooth areas between the suture and the pseudoepipleura; pseudoepipleura with transversal long dense horseshoe-shaped punctures. Humeral callus very developed and protuding outwards; articular area smaller than in *E. ignita*. Outer face of meso- and metatibiae with short impressed lines varying from longitudinal to transverse and short erect setae through the entire surface. Wings (Fig. 2a): vertical secondary sclerification of apical field thicker than in *E. ignita* and MP_{1+2} - RP loop distinctly longer. Spermatheca as in figs. 6e, f, g, h.

VARIABILITY

E. gestroi is less variable compared to the former species; the colours vary from bronze green to green with faint reddish sheen. In the pair from Lata Jarom the smooth elytral areas are very small, while punctures and lines are slightly more impressed.

DISTRIBUTION AND HABITAT

Recorded from Peninsular Malaysia, Sumatra and Borneo (Sabah and Sarawak).

Both species are found in rainforests, they are sympatric and sometimes also syntopic (Lata Jarom, leg. Jeniš). *E. ignita* seems to be restricted to lowland rainforests, where it has been collected by beating leaves or with window traps; *E. gestroi* shows a broader ecological range because it is found in both lowland and montane forests (till 2100 m a.s.l.), where it is the most commonly collected Ceratocanthidae. There are several records of this species at light. The unusual vestiture of galeal brush, which is covered by short and thick bi- or triphids dense setae (while in most other Ceratocanthidae these setae are longer, finer and usually sharp) could suggest that *Ebbrittoniella* has feeding habits different from the ones of the majority of Ceratocanthidae.

KEY TO THE SPECIES OF ***EBBRITTONIELLA***

1 Labrum distally distinctly truncate, truncature marked dorsally by a slight carina bearing a row of long, fine, erect setae, truncature in frontal view forming a plate irregularly elliptical or semicircular 2

\- Labrum without distinct truncature marked dorsally by a carina . . . . other Ceratocanthidae

2 Anterior angles of pronotum triangular; mesotibiae slender and relatively narrow (W/L ratio ≅ 0,2), with inner apical spur of ♂♂ bent inwards at a right angle; apex of protibiae usually ending with two teeth in the ♀♀ (one known exception); apical spur of protibiae strong, apically distinctly bent downwards . . . . *Cyphopisthes* Gestro

- Anterior angles of pronotum broadly rounded; mesotibiae short and wide (W/L ratio ≅ 0,3), with the inner apical spur of ♂♂ straight and extremely short; apex of protibiae ending with a single tooth in both sexes; apical spur of protibiae fine, very gently and regularly bent downwards. . . . . *Ebbrittoniella* Martínez

3 Surface of pronotum strongly punctured, punctures very dense, giving a granulose appearance, pronotal pubescence long, yellowish, recumbent, elytra with the same microsculpture and pubescence as pronotum, but with some smooth longitudinal areas, humeral callus very pronounced . . . . *E. gestroi* (Paulian)

- Surface of pronotum smooth, with sparse simple or horseshoe shaped punctures, glabrous or at most with very fine and short erect hyaline pubescence, elytra like pronotum, humeral callus weakly pronounced . . . . *E. ignita* (Westwood)

DISCUSSION

Some interesting new discoveries about the genitalia of the Ceratocanthidae were made during this revision. First of all it was found that the bursa copulatrix, which contains the spermatophore, bears a small subcircular sclerite on its inner wall, which probably has the function of breaking the spermatophore; similar sclerites have been observed in other genera of Ceratocanthidae, namely *Pterorthochaetes* Gestro, 1899 (Ballerio, 1999), *Philharmostes* Kolbe, 1895 and its allies (Ballerio, 2000) and *Eusphaeropeltis* Gestro, 1899 (author's unpublished data). Secondly a mobile accessory sclerite was detected, lying between the ventral basal extremities of parameres and associated with the median lobe; normally it lies parallel to the anchoring point of parameres with basal piece, but, when the internal sac is everted, the sclerite is raised at right angle, perpendicular to the anchoring point of parameres; it is possibly an intermediate form between an anchoring and a supporting sclerite (see D'Hotman & Scholtz, 1990).

In order to find the closest relationships of the genus *Ebbrittoniella* an analysis was conducted on all the genera of typical Ceratocanthidae, on the basis of all available morphological characters of adults, using the sister group of Ceratocanthidae, i.e. the Hybosoridae (Browne & Scholtz, 1996) and in particular the genera *Phaechrous* Castelnau, 1840 and *Liparochrus* Erichson, 1848 (Howden & Gill, 1995), as an out group for character polarization. The analysis suggests that *Cyphopisthes* Gestro, 1899 could be the genus closest to *Ebbrittoniella*. The following synapomorphies are shared by the two genera: a) outer edge of protibiae smooth (low magnification), b) sexual dimorphism involving the apical teeth of protibiae, c) labrum distally truncate, truncature marked dorsally by a slight carina bearing a row of erect fine setae, d) spermatheca strongly sclerotized and e) metathoracic wings: apical field with a vertical secondary sclerification near the radial cell. The genus *Cyphopisthes* can be divided into two groups, whose definition and status are being dealt with in a separate paper, *Ebbrittoniella* shares four further synapomorphies with the group formed by *C. acromialis*

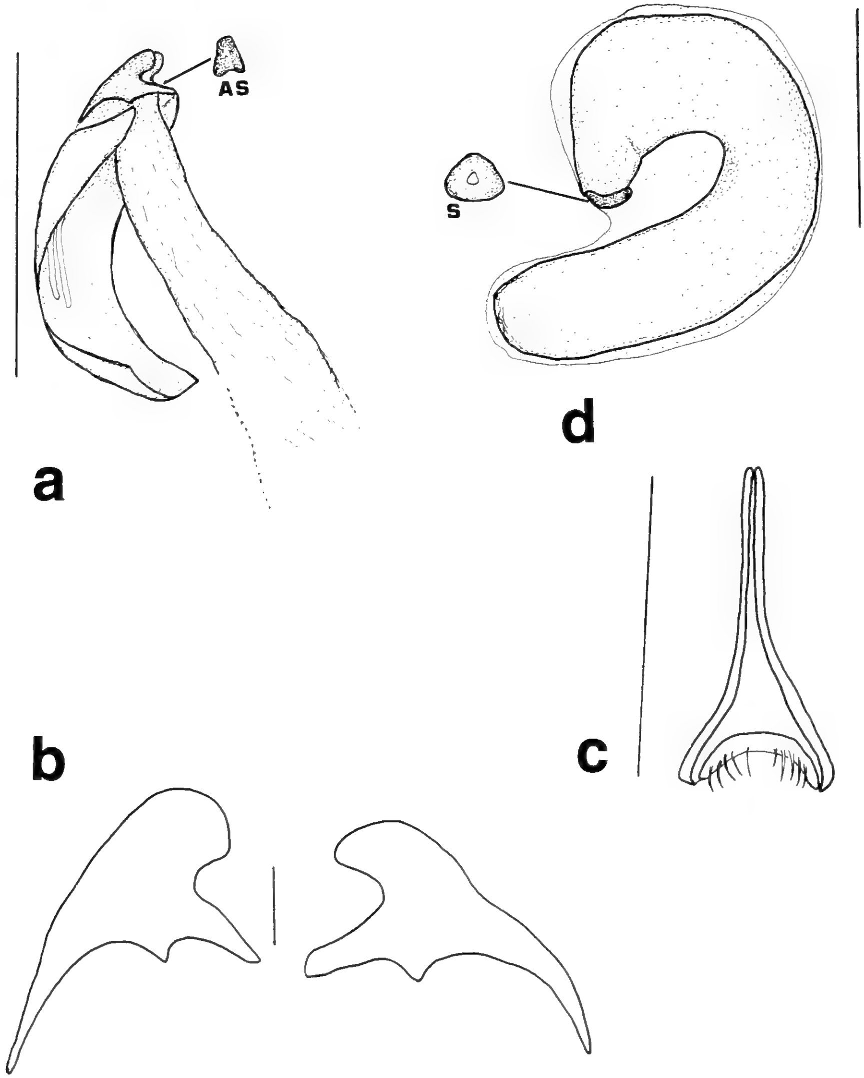

FIG. 5 – a: *E. gestroi* (Cameron Highlands), aedeagus with accessory sclerite (AS) (scale bar: 1 mm); b: *E. gestroi* (Cameron Highlands), parameres (lateral view) (scale bar: 0,1 mm); c: *E. gestroi* (Cameron Highlands) genital segment (scale bar: 1 mm); d: *E. gestroi* (Cameron Highlands), bursa copulatrix with sclerite (S) and spermatophore inside (scale bar: 1 mm).

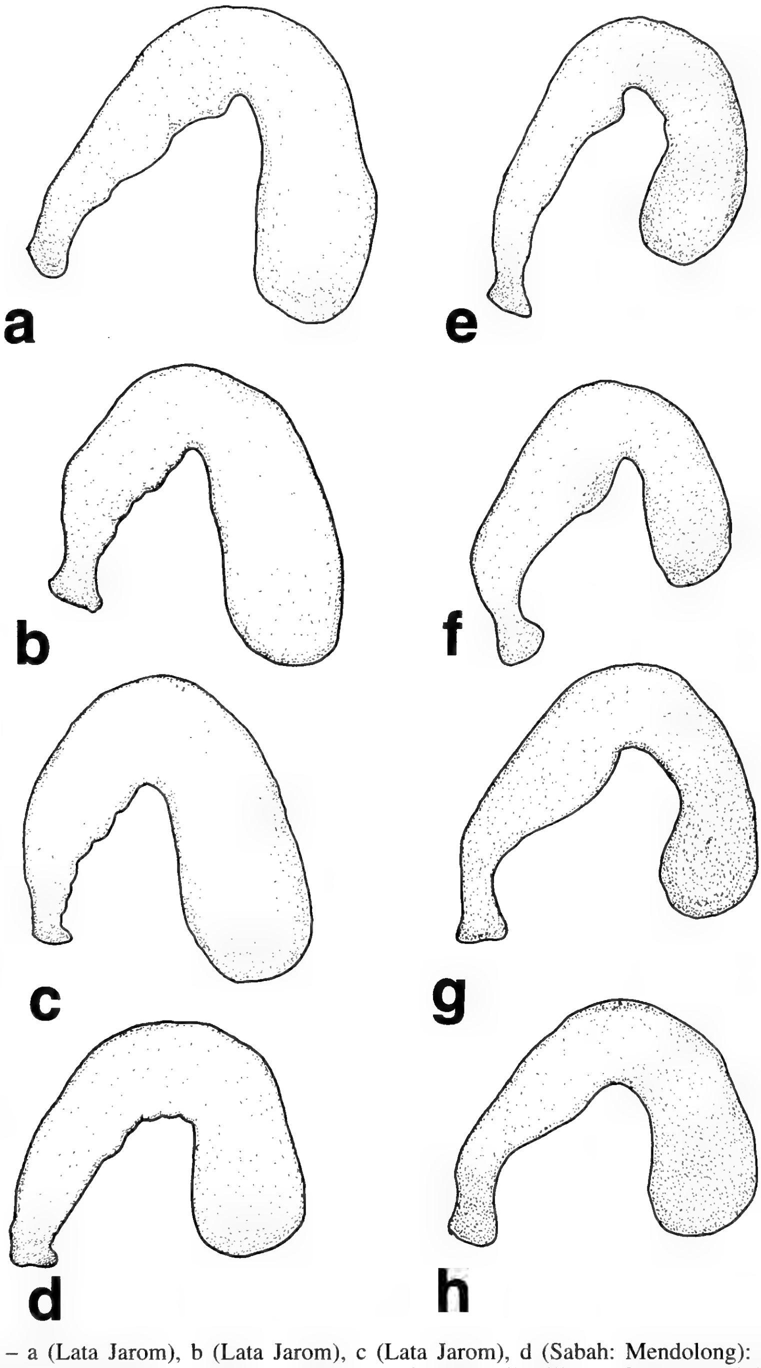

FIG. 6 – a (Lata Jarom), b (Lata Jarom), c (Lata Jarom), d (Sabah: Mendolong): *E. ignita*, spermatheca; e (Borneo: north of Kalabakan), f (Maxwell Hill), g (Cameron Highlands), h (Cameron Highlands): *E. gestroi*, spermatheca (scale bar: 0,1 mm).

(Pascoe, 1860) and few other species, i.e. f) labium with a very deep and wide regular-U-shaped excavation in the middle, g) spermatheca deeply U-shaped, h) bursa copulatrix with a characteristically shaped sclerite, and i) presence of an accessory sclerite among parameres. Characters b), c) and h) are autoapomorphic.

The similarities with *Ceratocanthus* White, 1842 stressed by earlier authors are likely due to convergent evolution and, although at the present stage of knowledge remote relationships cannot be excluded, there are several characters that place *Ebbrittoniella* and *Cyphopisthes* quite far from *Ceratocanthus*. The latter differs at least in the following characters: a) labrum neither abruptly truncate nor divided by any carina, b) elytra without a false epipleuron, c) metathoracic wings: MP_{1+2} – RP loop absent, d) metathoracic wings: apical field without vertical secondary sclerification, e) meso- and meta- tarsi capable of being folded along the longitudinal axis of the inner face of the tibia, f) sexual dimorphism not involving the shape of apical teeth of protibiae and g) spermatheca weakly sclerotized.

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I wish to thank the following people for permission to study material, loan of specimens, valuable information and advice: S. Adebratt (Frinnaryd, Sweden), D. Ahrens (SMTD), S. Bečvář (České Budějovice, Czech Republic), S. Bílý (NMPC), Y. Cambefort (MNHN), P. Čechovský (Brno, Czech Republic), G. Cuccodoro (MHNG), I. Jeniš (Nakló, Czech Republic), M.D. Kerley (BMNH), J. Krikken (RMNH), I. Löbl (MHNG), O. Martin (ZMUC), G. McGavin (OXUM), O. Merkl (HNHM), O. Montreuil (MNHN), R. Paulian (Bordeaux), R. Poggi (MCSN), G. A. Samuelson (BPBM), C.H. Scholtz (University of Pretoria), J. Scheuern (Westum, Germany), H. Schönmann (NHMW), R. Schuh (Katzelsdorf, Austria), C. Zorn (Dresden). R. Furlan (Centro C.U.G.A.S., Università di Padova) took SEM micrograph and J. Kobylák (Praha) executed the habitus drawings.

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A new desert psocid from Namibia (Insecta: Psocoptera: Trogiidae)

Charles LIENHARD
Muséum d'histoire naturelle, c. p. 6434, CH-1211 Genève 6, Switzerland.
E-mail: charles.lienhard@mhn.ville-ge.ch

A new desert psocid from Namibia (Insecta: Psocoptera: Trogiidae). - A single female of a new species representing a new genus of the family Trogiidae (Psocoptera: Trogiomorpha: Atropetae) is described and illustrated: *Spinatropos philippi* gen. n., sp. n. The specimen has been collected in an unusual biotope for Psocoptera, at Diaz Point (Lüderitz), on a rocky desert headland with hardly any vegetation.

Key-words: Psocoptera - Trogiidae - new genus - new species - desert fauna - Namibia.

INTRODUCTION

Almost nothing is known on Psocoptera of Namibia. The only psocid recorded from this country (from Windhoek) is the cosmopolitan and usually domestic species *Liposcelis bostrychophila* Badonnel, 1931 (cf. Checklist of Southern African Insects on Internet: http://www.ru.ac.za/departments/zooento/Martin/Insects.html).

The present material has been collected by N. P. & M. J. Ashmole under stones on a rocky desert headland with hardly any vegetation near Diaz Point (Lüderitz), a very unusual biotope for Psocoptera. These insects generally live on vegetation, mostly trees or shrubs, or in leaf-litter (cf. Lienhard, 1998a). An important factor which enables a psocid to live in the above mentioned biotope could be the proximity to the sea, which guarantees a constantly high relative humidity of the air. The occurrence of a psocid of the genus *Liposcelis* Motschulsky, 1852 on apparently "sterile" littoral limestone rocks in the Mediterranean (Cyprus) has been reported by Lienhard (1998b). It would be worthwhile for ecologists to pay more attention to psocids accidentally captured in such unusual situations.

Besides these ecological aspects the present material is also interesting from a taxonomic and perhaps ethological point of view. It represents a very characteristic new species of the family Trogiidae which cannot be placed in one of the hitherto known genera of this family. Its most striking diagnostic character, the presence of two short stout externoapical spurs on each of the somewhat elongated third valvulae (fig. 1) may prove to be connected with special ovipositional behaviour. As known up to now, all Psocoptera lay their eggs on the surface of a substrate (cf. Lienhard, 1998a). The new species, however, seems to be equipped to slightly dig in its eggs into a sandy soil.

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According to N. P. Ashmole (*in litt.*) there were small deposits of sand or fine rock fragments in the crevices of its habitat at Diaz Point. Similar digging spines on ovipositor are known in other insects, e.g. Diptera, where they are present in sand-dwelling Therevidae (cf. Irwin & Lyneborg, 1981: p. 514, fig. 22) or in the essentially dune-inhabiting species *Helina protuberans* Zett. (Muscidae), which lays its eggs into sandy soils (cf. Hennig, 1964: p. 209, Textfig. 46).

Spinatropos gen. n.

Diagnosis. Apterous, mesothorax in dorsal view about of same width as prothorax, metathorax distinctly wider. Body densely pubescent, excepting the almost bald postclypeus, which bears only a few peripheral hairs. Postclypeus of normal shape, not exceedingly bulging. Compound eyes well developed, hemispherical, with some small hairs in dorsal half, ocelli absent. Maxillary palpus (fig. 4) with fourth (terminal) segment (P4) of cylindrical shape, some stout setae present in apical half of P2, P3 and P4, no forked sensillum on P4. Laciniae symmetrically developed, lacinial tip tridentate, teeth diverging and well developed (fig. 3). Hind tibia with two apical spurs and two spurs on inner face in apical half. Pretarsal claw lacking preapical tooth, pulvillus long and slender, its tip slightly enlarged (fig. 6). 8th sternite of the female without sclerified knob which could be used in sound production (cf. Lienhard, 1998a: fig. 26m, *Trogium pulsatorium*). Third valvula (fig. 1) somewhat elongated, as typical of the family-group Atropetae, with spiny pilosity, two short stout externoapical spurs and one slender normal seta near tip. Second valvula (fig. 1) relatively well developed, reaching almost to the middle of the third valvula. Spermapore simple (fig. 5). Spermatheca with two oval parietal glands of about equal dimensions, situated close to each other in the proximal zone of the vesicle (fig. 7). Glands with numerous pores, no papillae (fig. 8). Spermatophore with very long tubular part (fig. 7). Male unknown.

Type species. *S. philippi* sp. n.

Etymology. Spina (lat.) = spine, an allusion to the particular pilosity of the third valvula. Atropos = one of the three Fates, the antique goddesses of destiny; *Atropos* Leach, 1815 is a synonym of *Trogium* Illiger, 1798 and gave rise to the family-group name Atropetae. In analogy to *Atropos* the new name is of feminine gender.

Discussion. See discussion of the type species.

Spinatropos philippi sp. n. Figs 1-8

MATERIAL

Holotype ♀. Namibia: Diaz Point (Lüderitz), rocky desert biotope with hardly any vegetation, relatively close to the sea, by visual seaching under stones, 30.XI.1994, leg. N. P. & M. J. Ashmole (sample nr 3090) (Muséum d'histoire naturelle de Genève).

ETYMOLOGY

The species is dedicated to N. Philip Ashmole, one of its collectors, in acknowledgement of his tireless efforts in collecting psocids in biotopes where they "should not occur".

DESCRIPTION (♀)

Coloration. Body, legs and antenna whitish to light brown. Compound eye black (after 4 years in alcohol). Apical half of flagellar segments darker brown than basal half in basal part of the antenna, flagellar segments in its apical part entirely brown.

Morphology. See generic diagnosis, with the following complements. Vertical and frontal sutures distinct. Both antennae damaged, one with 22, the other with 11 segments. Marginal sensilla of labrum (fig. 2) typical of the family Trogiidae (cf. Badonnel, 1977). The complete aptery of the specimen is real and not due to broken winglets. This is supported by the absence of insertion points of winglets and by the even pilosity of thoracic tergites (in the frequently encountered cases of micropterous or brachypterous Trogiidae where winglets are broken, insertion points are visible on mesothoracic tergite and the lateral parts of the metathoracic tergite are bald, as it has been figured for the genus *Cerobasis* Kolbe, 1882 by Lienhard, 1998a: fig. 24c). Mesothorax (in dorsal view) shorter than half width of vertex. No coxal organ differentiated. Femora somewhat thickened, hind femur about three times as wide as hind tibia. Hind tibia with some long hairs on outer face. First segment of hind tarsus with numerous stout spur-like setae on ventral face. Epiproct bald in the middle, with some lateral hairs. Paraprocts with a distinct anal spine on hind margin. Subgenital plate absent, ovipositor valvulae basally covered by some membraneous folds. The wall of the spermathecal vesicle bears numerous fine pores, especially in the more distal half (fig. 7). The length of the oval spermathecal glands is about 125 μm, each gland bears much more than 100 pores (fig. 8).

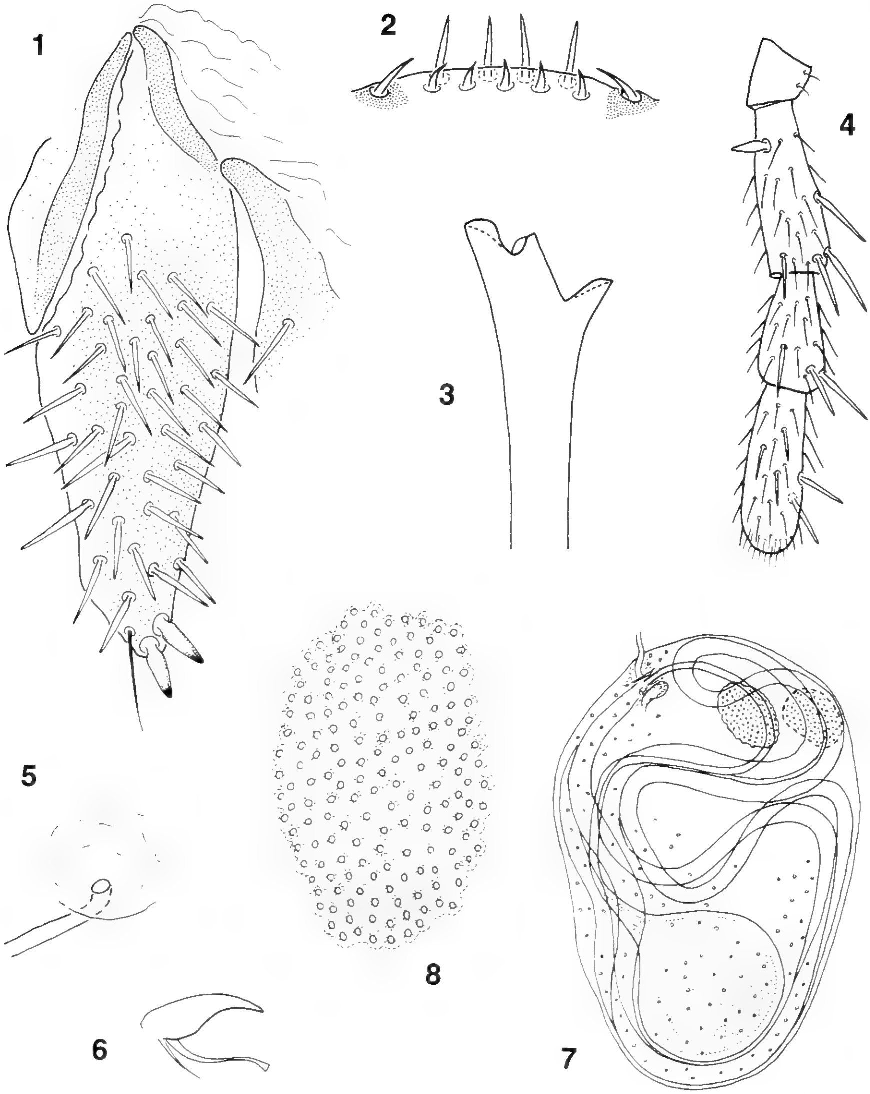
Measurements. Body length = 2,0 mm. Vertex (width of head capsule) = 650 μm. Length of hind femur = 520 μm. Length of hind tibia = 750 μm. Length of hind tarsomeres (measured from condyle to condyle): t1 = 320; t2 = 72; t3 = 90.

Remark. The male is not yet known, but the presence of a spermatophore in the spermatheca of the female gives evidence of the bisexuality of the species.

DISCUSSION

Within the family Trogiidae (sensu Smithers, 1990) the new genus is characterized by the very particular spiny pilosity of the third valvula, especially by the presence of two stout externoapical spurs, but also by the cylindrical shape of the terminal segment (P4) of the maxillary palpus. In all other non-fossil genera, P4 is at least slightly enlarged apically, often much enlarged (hatchet-shaped). In the genera where females are known (not known in *Anomocopeus* Badonnel, 1967) the pilosity of the third valvula consists of normally shaped slender setae, as usual in the family-group Atropetae. The genus can also be distinguished from most of the other genera (amber fossils included) by its complete aptery. The only other apterous genera are *Anomocopeus* and *Mymicodipnella* Enderlein, 1909; some apterous species are also known in the large genus *Cerobasis*.

Nothing exact is known about the biology of the new species, for some general remarks, see the introduction.



FIGS 1-8

Spinatropos philippi gen. n., sp. n., female: 1, ovipositor valvulae; 2, marginal sensilla of labrum; 3, lacinial tip; 4, maxillary palpus; 5, spermapore; 6, pretarsal claw; 7, spermatheca, containing one spermatophore; 8, parietal gland of spermatheca.

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I am very grateful to N. Philip and Myrtle J. Ashmole (Edinburgh) for having made their Namibian collections of psocids available to me. I also thank N. P. Ashmole for reading the manuscript and making some valuable suggestions. I am indebted to my colleague Bernhard Merz (Geneva) for information about the presence of digging spines on the ovipositor in Diptera.

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Terrestrial Isopoda from Guatemala and Mexico (Crustacea: Oniscidea: Crinocheta)

Andreas LEISTIKOW
Universität Bielefeld
Abteilung für Zoomorphologie und Systematik
Morgenbreede 45
D-33615 Bielefeld.
E-mail: Leiste@Biologie.Uni-Bielefeld.de

Ruhr-Universität Bochum
Lehrstuhl für spezielle Zoologie
Universitätsstraße 150
D-44780 Bochum.

Terrestrial Isopoda from Guatemala and Mexico (Crustacea: Oniscidea: Crinocheta). - Some terrestrial Isopoda from Mexico, described in the genus *Philoscia* Latreille, 1804, are redescribed and transferred to other genera. Two new genera, *Quintanoscia* gen. n. and *Oxalaniscus* gen. n. are described, they belong to the most primitive representatives of the Oniscoidea within the Crinocheta. One of the species, *Androdeloscia formosa* (Mulaik, 1960) is recorded from Guatemala for the first time. A closely related species, *A. valdezi* sp. n. is described as new to science. New records for *Littorophiloscia denticulata* (Ferrara & Taiti, 1981) and *Burmoniscus kohleri* (Schmalfuss & Ferrara, 1978) are presented; they were recorded in the New World for the first time. Their distributional patterns and phylogenetic relationships are discussed.

Key-words: Crustacea - Oniscidea - *Philoscia* - *Androdeloscia* - *Littorophiloscia* - *Burmoniscus* - new genera - new species - Central America - taxonomy.

INTRODUCTION

Central America is one of the regions of the world, which is almost unexplored with respect to the terrestrial isopod fauna. Only few contributions deal with taxa of Oniscoidea collected in this biogeographically interesting area, as e.g., Miers (1877) reporting on some Oniscidea from Central America. Particularly isopods of the northern countries, Mexico and Guatemala, are little known. Richardson (1907) described a new scleropactid species *Spherarmadillo schwarzi* Richardson, 1907, from Guatemala and later a species of Armadillidae, *Globarmadillo armatus* Richard-

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son, 1910 was described by Richardson (1910). This work remains the only contribution to the Guatemalan oniscidean fauna.

The exhaustive contribution of Mulaik (1960) on the terrestrial isopod fauna of Mexico is an important work, although the taxonomy used was no more up to date in 1960. Many species placed in the genus *Philoscia* Latreille, 1960 do not show any apomorphic character in common with, e.g., the European *Philoscia muscorum* (Scopoli, 1793), which is a typical member of this genus. Some of the species included in *Philoscia* are among the most primitive representatives of Oniscoidea as defined by Schmalfuss (1989): they, for instance, lack the noduli laterales. Some species of *Philoscia* were revised in this study and transferred to other genera.

More recently, Schultz (1977) contributed to our knowledge of the troglobitic species of Oniscidea from Central America, with *Troglophiloscia laevis* Schultz, 1977 being added to the Mexican fauna. The species is related to the Cuban *T. silvestrii* Brian, 1929, the type of the genus (Brian, 1929). The species might also occur in northern Guatemala, as there are many caves in the northern province Petén, which might be suitable habitats for this genus. However, it was not found in the Cueva Actún Can near Santa Elena, Petén in a recently started survey.

This study aims to increase our knowlegde on the crinochete Oniscidea , which are of philosciid appearance. Several species are described in detail to get access to a complete data set for a phylogenetic analysis. New data are given for some species probably introduced to Guatemala. Both *Littorophiloscia denticulata* (Ferrara & Taiti, 1981) and *Burmoniscus kohleri* (Schmalfuss & Ferrara, 1978) are recorded for the first time from the New World. Ther distribtional patterns and phylogenetic relationships are discussed.

The material examined is deposited in: Instituto Politécnico Nacional de México (IPNM), Staatliches Museum für naturkunde (SMNS), Muséum d'histoire naturelle de Genève (MNHG), Universidad del Valle de Guatemala (UVG) and in the author's collection.

SPECIES ACCOUNT

Quintanoscia gen. n.

DIAGNOSIS: Cephalothorax without linea frontalis and linea supra-antennalis; lamina frontalis present; compound eyes composed of 12 ommatidia; antennula composed of three cylindrical articles; antennal flagellum three-articulate with apical organ bearing two short free sensilla.

Mandibles with molar penicil consisting of three branches; medial endite of maxillula with two penicils and apical tip; lateral endite with 4+6 teeth and slender stalk; lobes of maxilla subrectangular; densely covered with trichiae; maxilliped basipodite without sulcus lateralis; palp three-articulate; proximal article with two long setae; medial and distal article with prominent setal tufts; endite elongate; setose; with long penicil rostrally.

Pereopods stout; antenna-grooming brush of carpus 1 arranged longitudinally; dactylus with long inner claw; dactylar seta ending in a knob; coxal plates without sulcus marginalis and gland pores; noduli laterales present; quite similar to tricorn-like setae; insertion on all coxal plates at same distance from lateral margin.

Pleopods with rhomboidal exopodites bearing sensory spines laterally; endopodites subquadrangular; no respiratory areas discernible at 400x magnification; male genital papilla with ventral shield.

Uropod with protopodite laterally grooved; exopodite twice as long as the more proximally inserted endopodite.

TYPE SPECIES: *Philoscia contoyensis* Mulaik, 1960 (by monotypy).

NUMBER OF NOMINAL SPECIES: only type species.

ETYMOLOGY: The genus is named after the Mexican province Quintana Roo, where the type species was collected.

DISTRIBUTION: Only known from southeastern Mexico on the Yucatán Peninsula.

REMARKS: The genus *Quintanoscia* gen. n. is close to the groundpattern of the Oniscoidea, the shape of the maxilliped is similar to *Deto* Guérin, 1836 and *Alloniscus* Dana, 1852. The pereopod 1 is equipped with a longitudinal carpal brush and the medial margin is bearing several bifid sensory spines. The autapomorphies of the genus are:

- Reduction of the lateral lobes [lateral lobes present]
- *Cephalothorax* broadened [*vertex* not broader than height of *cephalothorax*]

The coxal plates bear several tricorn-like setae. One of those setae bears a distinctly longer sensillum, which is twice as long as the basal cuticular plaque. This structure can be interpreted as a nodulus lateralis.

Quintanoscia contoyensis (Mulaik, 1960) Figs 1-6

Philoscia contoyensis Mulaik, 1960

Material: Paratypes, 5 ♂ (max. body length 3.5 mm): Mexico, Quintana Roo, Isla Contoy, leg. 20.XI.1947, B.F. Osorio Tafall, IPNM 1631-A.

Colour: Mulaik (1960) wrote in the original description: "La coloración de los ejemplares conservados en alcohol; es un moteado de café; rojizo y armadillo. El color más obscuro está confiando a una franja dorsal; media; delgada e irregular; a una area angosta a lo largo de los márgenes de os epimeros y entre estas; a otra banda más angosta fragmentada en manchas. La region ventral es casi blanca. Las formes jovenes muestran menos pigmento que los adultos."

Cephalothorax: Rather large with regard to body length; compound eyes bearing 12 ommatidia; vertex strongly arched; no linea frontalis and linea supra-antennalis visible; lamina frontalis inconspicuous (fig. 1; Ctf).

Pereon: Tegument smooth and shiny; bearing evenly spread tricorn-like setae; noduli laterales similar to tricorn-like setae; sensillum comparatively longer; on all coxal plates insertion at same distance to lateral margin; more distally located from plate I to VII; no sulcus marginalis and gland pores.

Pleon: Rather short; narrower than pereon; prominent neopleurae on pleonites III to IV; pleotelson half as long than pleon; triangular; bordered by tricorn-like setae.

Appendages:

Antennula: Three-articulate with cylindrical articles; distal article bearing longitudinally arranged aesthetascs (fig. 1; An1).

Antenna: Peduncle covered with tricorn-like setae; flagellum three-articulate; medial and distal article with pair of aesthetascs; apical organ as long as medial article; with short free sensilla (fig. 5; An2).

Mouth parts as described in generic diagnosis (fig. 2).

Pereopods: Rather stout; carpus 1 with longitudinal antenna-grooming brush; medial border of carpus and merus 1 to 4 bearing many bifid sensory spines (fig. 3-5; PE1-7); dactylus with medium-sized inner claw (fig. 3; Dac); stout interungual seta; tricorn-like seta laterally; dactylar seta with knob-like tip (fig. 4; Sd5). Sexual dimorphism: Due to the lack of females not observed.

Pleopods: Exopodites rhomboidal with lateral margin bearing four to ten sensory spines; on pleopod 4 and 5 one subapically on medial border; pleopod 5 with small pectinate scales caudally; not arranged in rows; endopodites rounded triangular to quadrangular; respiratory areas not discernible at 400x magnification (fig. 6; PL1-5). Sexual dimorphism: Pleopod 1 endopodite long; rather prominent with ill-defined basal area containing the intrinsic endopodite 1 levering muscle M49 (Erhard, 1997); no row of small spines medio-caudally (fig. 6; PL1); pleopod 2 exopodite with lateral margin slightly more sinuous than on exopodite 3; endopodite twice as long as exopodite; rather stout (fig. 6; PL2).

Uropod: Protopodite triangular with lateral groove; endopodite inserting more proximally than two times longer exopodite (fig. 5; UR).

Genital papilla: Ventral shield with parallel margins in basal half; slightly surpassed by orifices (fig. 6; Gen).

Oxalaniscus gen. n.

Diagnosis: Cephalothorax with lamina frontalis; linea supra-antennalis and lateral lobes; linea frontalis reduced; compound eyes composed of about nine ommatidia. Antennula three-articulate; slender; antenna with three-articulate flagellum (Mulaik, 1960).

Mandible with molar penicil composed of three branches; lateral endite of maxillula with 4+5 simple teeth; slender stalk present; maxilla subrectangular; maxilliped with long penicil on endite and prominent setal tufts on palp.

Pereopods with coxal plates lacking distinct nodulus lateralis; carpus 1 with longitudinal carpal brush; setal brushes composed of sensory spines; not very dense; present on carpus and merus 1 to 5; dactylar seta apically spatuliform.

Pleopods with prominent exopodites bearing few sensory spines laterally; no respiratory structures discernible.

Uropod with protopodite subtriangular carrying lateral groove; endopodite inserting slightly proximally of exopodite. Genital papilla with ventral shield surpassed by terminal spatula.

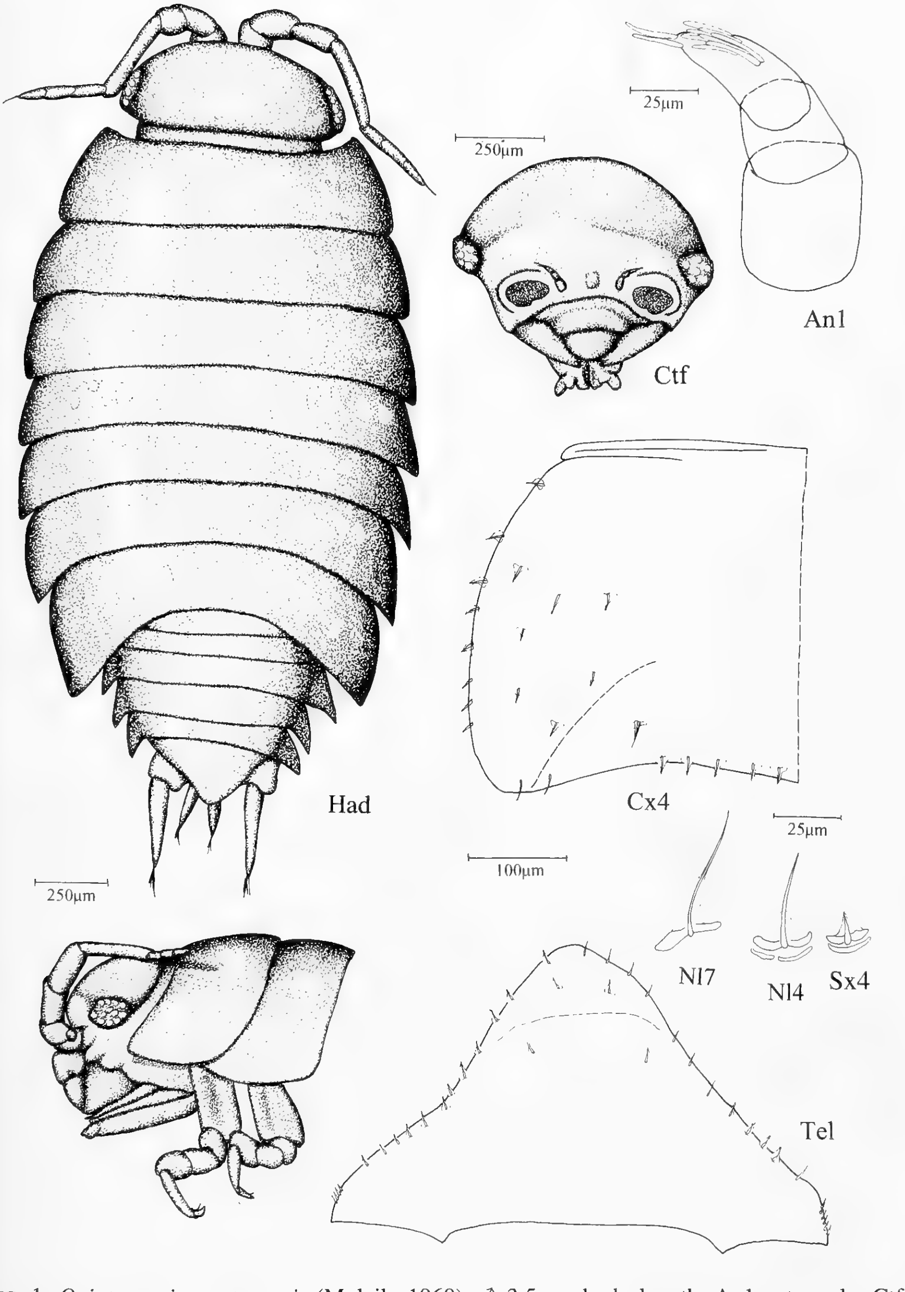

FIG. 1: *Quintanoscia contoyensis* (Mulaik, 1960), ♂ 3.5mm body length. An1 antennula; Ctf cephalothorax in frontal view; Cx4 coxal plate IV; Had habitus in dorsal view; Hal habitus in lateral view; Nl4/7 setae of nodulus lateralis shape from coxal Figures IV and VII; Sx4 tricorn-like seta of coxal plate IV; Tel pleotelson.

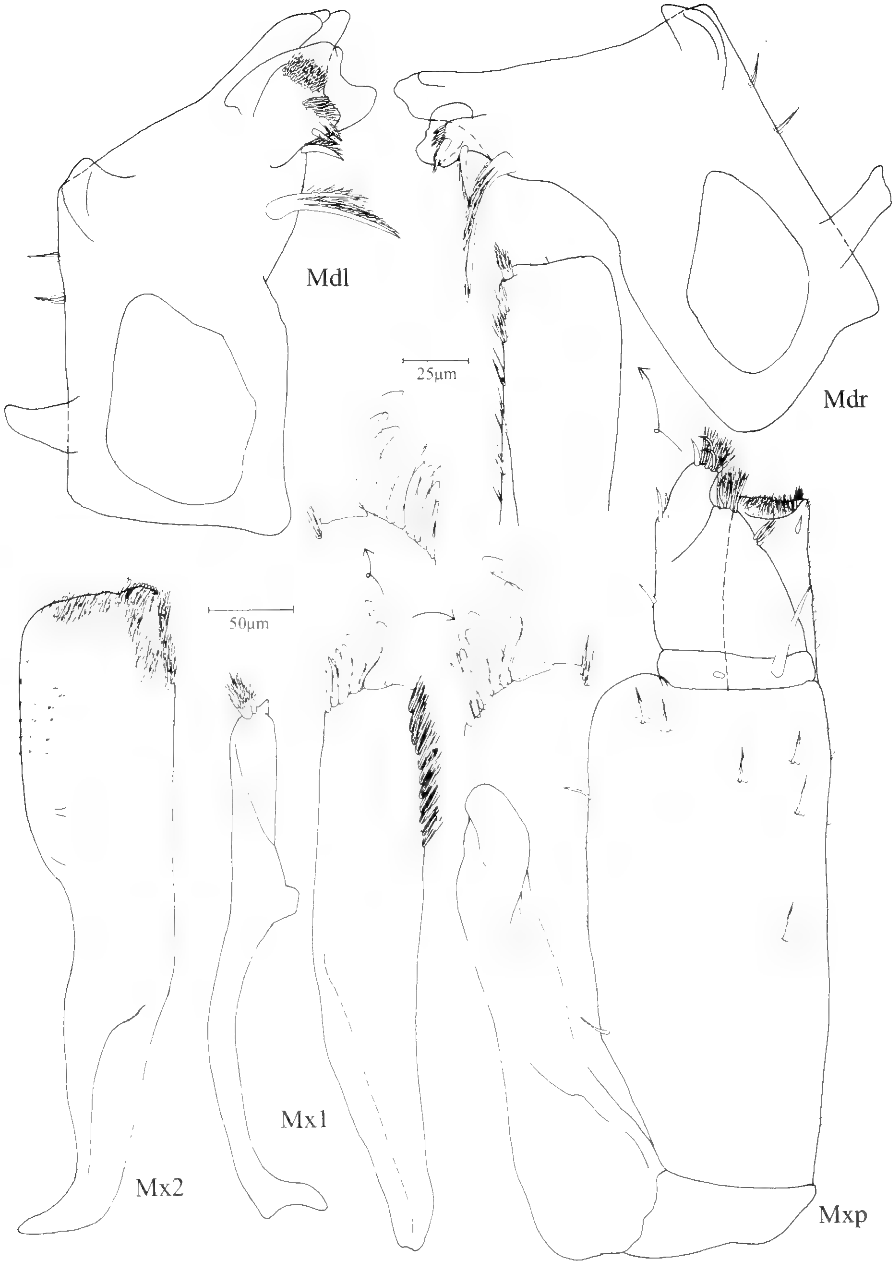

FIG. 2: *Quintanoscia contoyensis* (Mulaik, 1960), ♂ 3.5mm body length. Mdl/r left and right mandible; Mxp maxilliped, with detail of endite in rostral view; Mx1 maxillula, with details of apical lateral endite in caudal and rostral view; Mx2 maxilla.

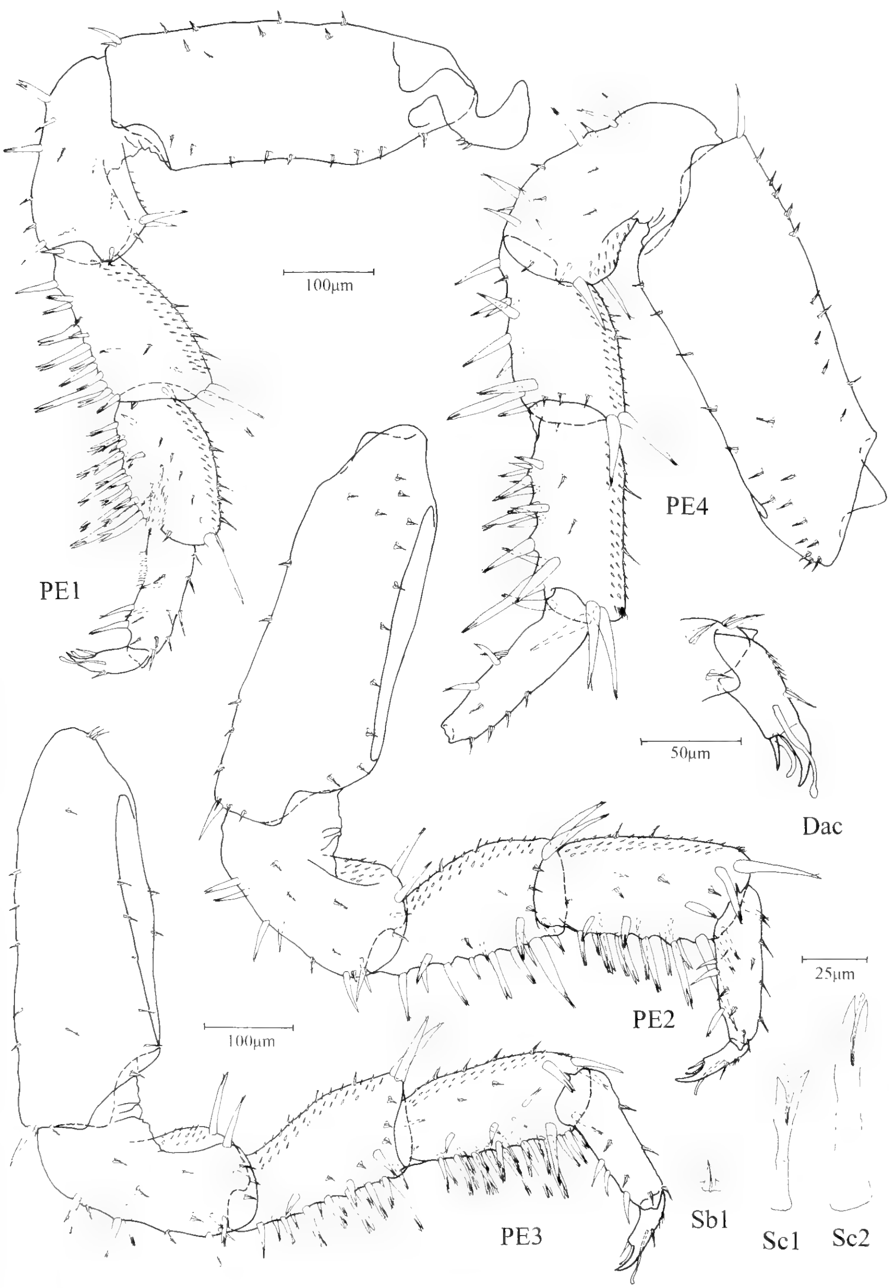

FIG. 3: *Quintanoscia contoyensis* (Mulaik, 1960), ♂ 3.5mm body length. Dac dactylus of pereopod 1 in rostral view; PE1-4 pereopods 1 to 4, in rostral (PE1) or caudal (PE2-4) view; Sb1 tricorn-like seta of basis 1; Sc1 sensory spine of carpal brush; Sc2 sensory spine of carpus 2.

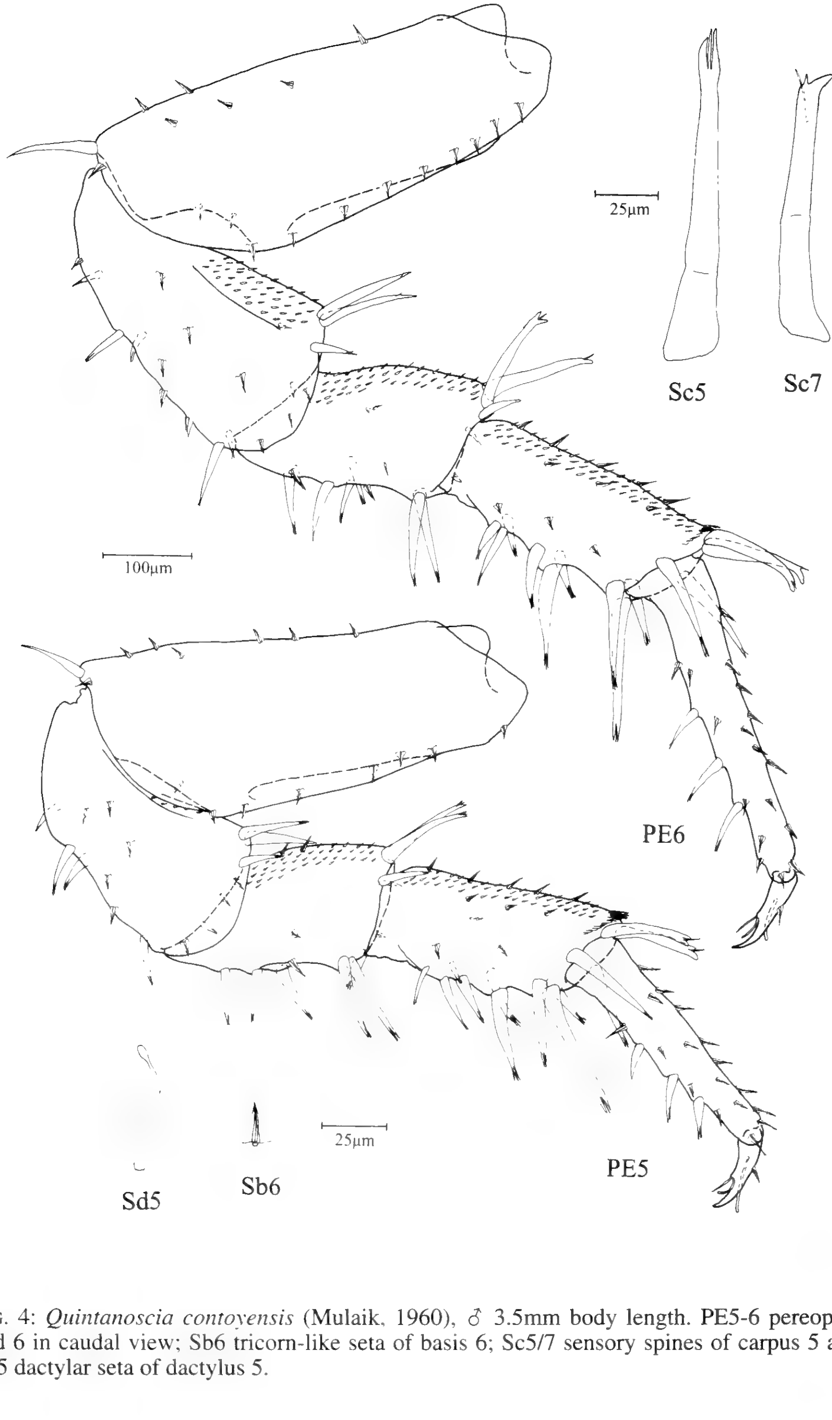

FIG. 4: *Quintanoscia contoyensis* (Mulaik, 1960), ♂ 3.5mm body length. PE5-6 pereopods 5 and 6 in caudal view; Sb6 tricorn-like seta of basis 6; Sc5/7 sensory spines of carpus 5 and 7; Sd5 dactylar seta of dactylus 5.

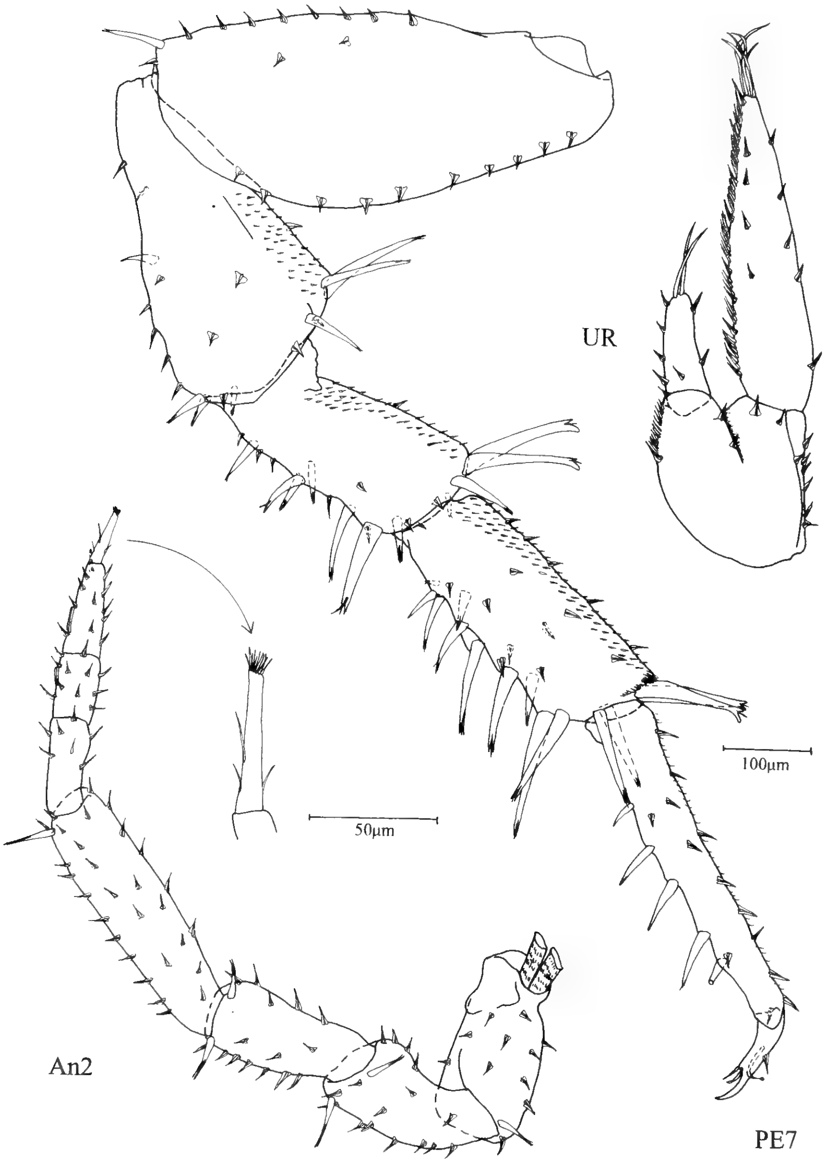

FIG. 5: *Quintanoscia contoyensis* (Mulaik, 1960), ♂ 3.5mm body length. An2 antenna, with detail of apical organ; PE7 pereopod 7 in caudal view; UR uropod in rostral view.

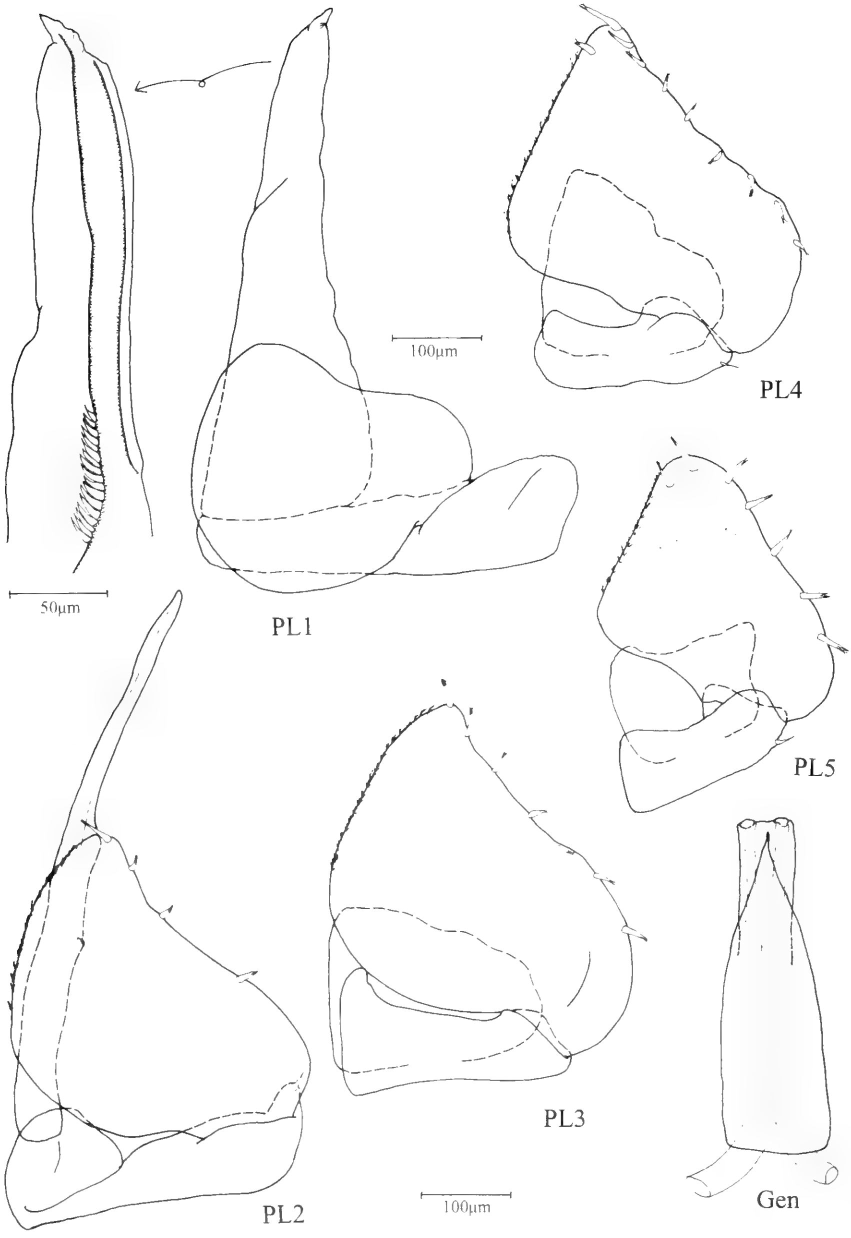

FIG. 6: *Quintanoscia contoyensis* (Mulaik, 1960). ♂ 3.5mm body length. Gen genital papilla; PL1-5 pleopods 1 to 5 in rostral view, with detail of endopodite 1 in caudal view.

TYPE SPECIES: *Philoscia ctenoscoides* Mulaik, 1960 (by monotypy).
NUMBER OF NOMINAL SPECIES: only type species included.
ETYMOLOGY: The genus name is derived from oxalá, the god of creation of the indígenas from Brazil.
REMARKS: The genus *Oxalaniscus* gen. n. belongs to the most basal species of the taxon Oniscoidea. It seems closely related to *Quintanoscia* gen. n. The putative synapomorphies are given above. The following characters are the autapomorphies of this genus:

- Slender stalk of maxillula in a more lateral position [slender stalk medially, surrounded by group of lateral teeth]

In all other taxa with a slender stalk on the maxillula, it is in a medial position on the apical region, surrounded by the medial teeth of the outer group.

Oxalaniscus ctenoscoides (Mulaik, 1960) Figs 7-10

Philoscia ctenoscoides Mulaik, 1960

Material: several specimens: Mexico, Chiapas, Ruinas de Palenque, leg. 13.VII.1949, C. and M. Goodnight, Finca Guautimoc, leg. 02.VII.1950, C. and M. Goodnight; Tabasco, Emiliano Zapata, leg. 15.VIII.1945; Quintana Roo, Puerto Morelos, leg. XI.1947, B.F. Osorio Tafall, Isla Cozumel, leg. 24.XI.1947, B.F. Osorio Tafall, IPNM 1628.

Colour: "Dorso brillante e intensamente moteado con café" (Mulaik, 1960).

Cephalothorax: Wider than high with linea supra-antennalis and lamina frontalis; small lateral lobes present; compound eyes composed of about nine ommatidia (fig. 7, Ctf).

Pereon: Tegument smooth with few tricorn-like setae; coxal plates without gland pores; sulcus marginalis present; no noduli laterales visible (fig. 7, Cx4).

Pleon: Only slightly narrower than pereon; with prominent neopleurae on pleonite 3 to 5; pleotelson with rounded apex; lateral margins straight.

Appendages:

Antennula: Slender; composed of three articles; distal one cylindrical with apical pair of aesthetascs and medial set of about four aesthetascs (fig. 7, An1).

Antenna: Peduncle with scattered tricorn-like setae; flagellum broken in all the material examined; thus nothing can be said about the shape and the apical organ. According to Mulaik (1960) it is composed of three articles.

Mouth parts as decribed in generic diagnosis (fig. 8).

Pereopods: Rather stout (fig. 9; PE1-7); carpus without latero-distal setal tuft; no ornamental sensory spine on carpus 1; antenna-grooming brush longitudinal; carpus and merus 1 to 5 with loose brush of sensory spines; dactylus with short inner claw (fig. 9, Dac); all interungual setae broken in material examined; dactylar seta with flattened spatuliform apex (fig. 9, Sd1).

Pleopods: Exopodites of pleopod 3 to 5 large; bearing one to two sensory spines laterally; no respiratory areas discernible in light microscope; endopodites subrectangular (fig. 10, PL1-5). Sexual dimorphism: Male pleopod 1 exopodite obtusely triangular; endopodite more than two times longer than exopodite; slightly

bent sidewards; apex strongly bent sidewards with subterminal protrusions; about five to ten small spines at proximal end of spermatic channel (fig. 10, PL1). Pleopod 2 exopodite triangular with single latero-distal sensory spine; distal third of endopodite lace-shaped; slightly bent (fig. 10, PL2).

Uropod: As described in generic diagnosis.

Genital papilla: Ventral shield surpassed by terminally ending orifices; apex indistinctly truncate (fig. 10, Gen).

REMARKS: The two new genera *Quintanoscia* and *Oxalanoiscus* from Mexico are quite primitive with respect to several characters: They bear a subrectangular maxilla, the maxillipedal palp is equipped with very prominent setal tufts and the penicil of the endite is still prominent. Nonetheless, they are united in an sistergroup relationship due to the following synapomorphies:

- ■ Cephalothorax with linea frontalis reduced [linea frontalis present]
- ■ Molar penicil composed of three branches [molar penixcil composed of about ten branches]
- ■ Lateral endite of maxillula with 6+4 teeth, one of the inner set absent or at least vestigial [no tooth reduced in size]
- ■ Maxillular teeth simple [teeth of inner set cleft]

In the outgroup, represented by *Ligia baudiniana* Milne Edwards, 1840, *Deto echinata* Guérin, 1836 several species of Scleropatidae and *Alloniscus* Dana, 1852, the characters differ considerably. The mandible is bearing a penicil of about ten unfused branches and the maxillular teeth of the inner set are cleft or ctenate. Therefore, the character states in both new genera are interpreted as being derived.

In spite of their close relationship, each species is placed in a monotypic genus since the structure of the dorsal tricorn-like setae and the cephalothorax are striking. Probably *Quintanoscia* and *Oxalaniscus* are as distant to each other as they are to *Alloniscus*. In recent works on terrestrial isopods, the following characters are mostly used for generic separation: cephalothorax morphology, structure and position of dorsal receptors, presence of a sulcus marginalis, structure of the maxilliped, arrangement of the teth on the lateral endite of the maxillula, setal patterns of the pereopods, shape of pleon and pleotelson, shape of the male pleopod 5 and genital papilla (Vandel, 1973a, 1973b; Taiti & Ferrara, 1980). Therefore, a generic separation of the two taxa seems plausible.

Genus ***Littorophiloscia*** Hatch, 1947

DIAGNOSIS: Cephalothorax with linea supra-antennalis; slight lamina frontalis and lateral lobes; linea frontalis lacking; compound eyes composed of about 15 ommatidia. Antennula three-articulate; slender; antenna long with three-articulate flagellum; apical organ longer than distal article.

Mandible with molar penicil consisting of about ten free branches; maxillula with lateral endite bearing 4+6 teeth; inner set with five teeth cleft; slender stalk present; maxilla with both lobes subequal in width; maxilliped with endite setose; bearing prominent penicil rostrally; palp three-articulate; with three prominent setal tufts.

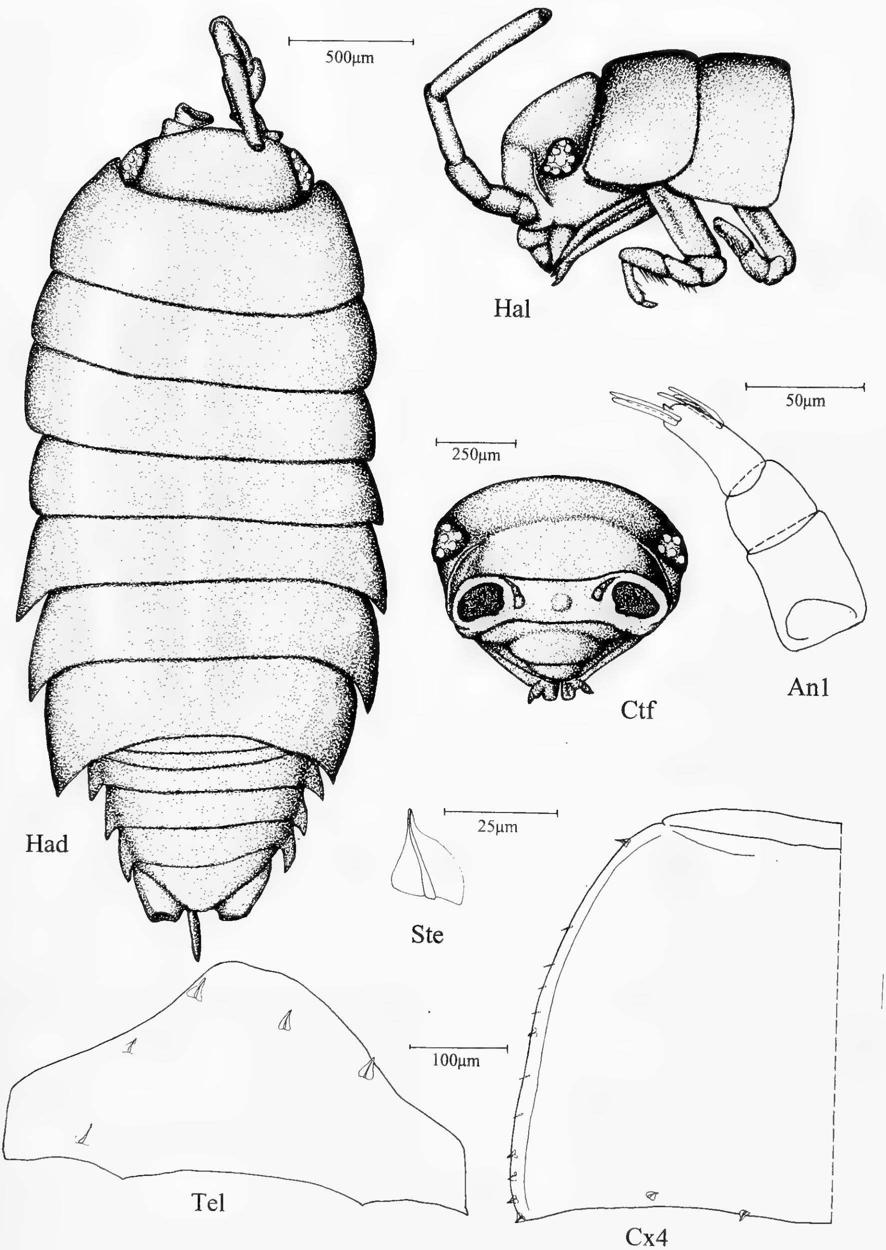

FIG. 7: *Oxalaniscus ctenoscoides* (Mulaik, 1960), ♂ 3mm body length. An1 antennula; Ctf cephalothorax in frontal view; Cx4 coxal plate IV; Had habitus in dorsal view; Hal habitus in lateral view; Ste tricorn-like seta of pleotelson; Tel pleotelson.

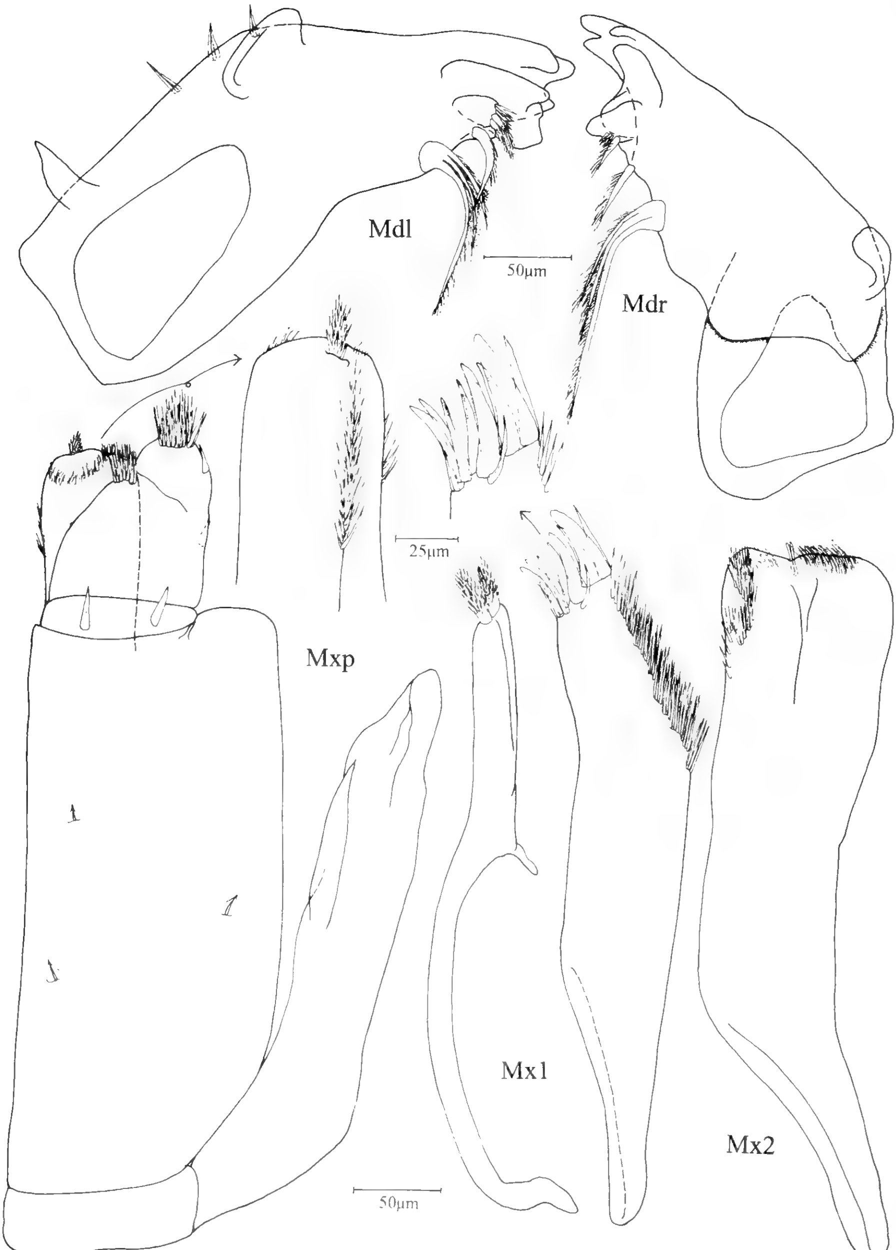

FIG. 8: *Oxalaniscus ctenoscoides* (Mulaik, 1960), ♂ 3mm body length. Mdl/r left and right mandible; Mxp maxilliped, with detail of endite in rostral view; Mx1 maxillula, with detail of apical lateral endite in rostral view; Mx2 maxilla.

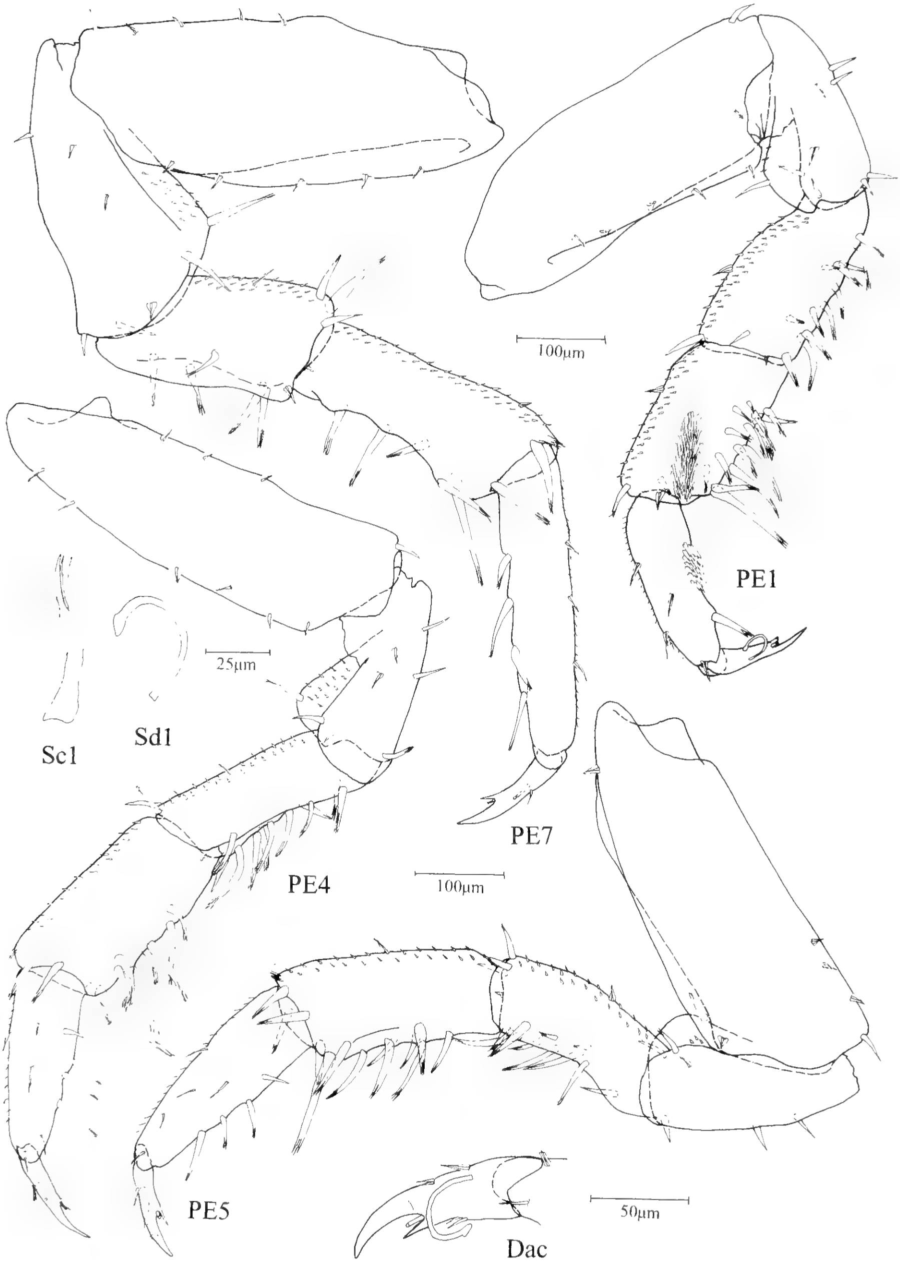

FIG. 9: *Oxalaniscus ctenoscoides* (Mulaik, 1960), ♂ 3mm body length. Dac dactylus of pereopod 1; PE1-7 pereopods 1 to 7 in rostral (PE1) or caudal view; Sc1 sensory spine of carpal brush; Sd1 dactylar seta of pereopod 1.

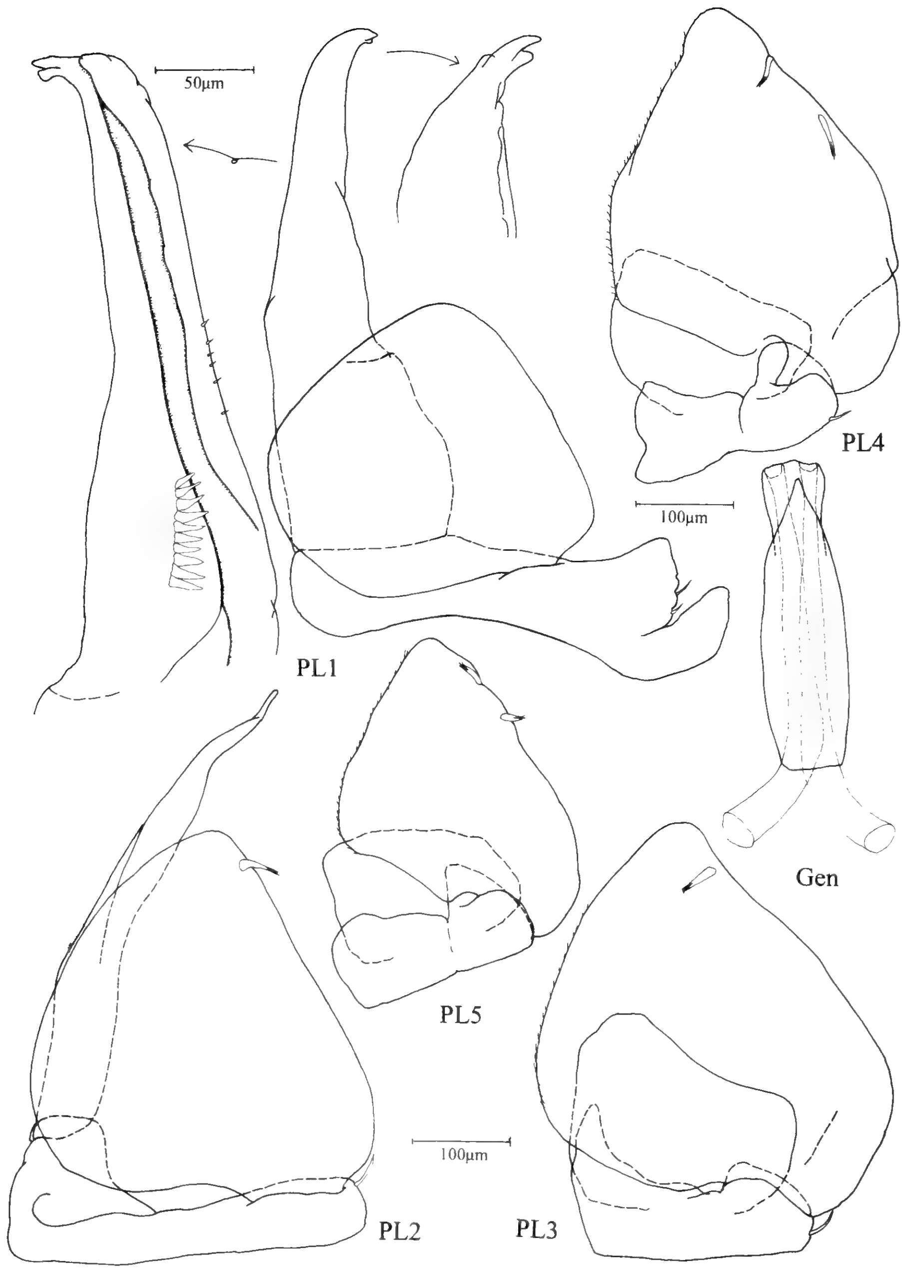

FIG. 10: *Oxalaniscus ctenoscoides* (Mulaik, 1960), ♂ 3mm body length. Gen genital papilla; PL1-5 pleopods 1 to 5 in rostral view, with detail of endopodite 1 in caudal and rostral view.

Pereopods slender; ornamental sensory spine of carpus 1 with serrate double-fringe; dactylus with interungual seta long; more conspicuous than dactylar seta; inner claw short; coxal plates without gland pores; sulcus marginalis and nodulus lateralis present; all noduli inserted at same distance from lateral margin. Male pereopod 1 propus and carpus inflated; bearing more or less prominent setal brushes.

Pleopods without respiratory areas; exopodites with about five sensory spines laterally; endopodites bilobate. Uropod with protopodite laterally grooved; endopodite inserting more proximally than exopodite.

Genital papilla with short ventral shield; orifices on small to conspicuously elongate protrusions of the terminal spatula.

TYPE SPECIES: *Philoscia richardsonae* Holmes & Gay, 1904.
NUMBER OF NOMINAL SPECIES: 23, four known from the Neotropics.
REMARKS: Taiti & Ferrara (1986a) revised the genus and gave a diagnosis for it, they stressed the similarity of the male pereopods 1 and the mouth parts in *Littorophiloscia* and *Halophiloscia* Verhoeff, 1908. With respect to the mouth parts, the polatity of the characters was misinterpreted; they are of a plesiomorphic character state in both genera, similar to the above described genera *Quintanoscia* and *Oxalaniscus*, and to other Crinocheta with a position basal to the Oniscoidea sensu Schmalfuss (1989).

Littorophiloscia denticulata (Ferrara & Taiti, 1981) Figs 11-14

Bilawrencia denticulata Ferrara & Taiti, 1981

Material examined: 3 ♂, 9 ♀ (ovigerous), 3 juveniles: Guatemala, Izabal, Lívinston, beach north of mouth of Rio Quegueche, between shells and fibres of coconuts, under *Ipomoea* sp., leg. 22.X.1998, A. Leistikow, MNHG and author's collection.

Colour: Dorsally light violaceous brown with white paramedian patches; coxal plates with two to three white patches; cephalothorax densely spotted with white; pleon uniformly violaceous brown.

Cephalothorax: Linea frontalis reduced; linea supra-antennalis; lamina frontalis and small lateral lobes present; compound eyes comprising eight ommatidia (fig. 11, Ctf).

Pereon: Slightly arched; coxal plates with sulcus marginalis and nodulus lateralis; distance between noduli and lateral margin subequal on all coxal plates (fig. 11, Cx4/Cxp); scattered tricorn-like setae present.

Pleon: Narrower than pereon; small neopleurae on pleonites 3 to 5 present; pleotelson rounded with few tricorn-like setae along margin.

Appendages:

Antennula: Long and slender; three-articulate with pairs of aesthetascs in a rowon distal article (fig. 11, An1).

Antenna: Slender sparsely covered with of tricorn-like setae; flagellum three-articulate with long apical organ; bearing short free sensilla; being as long as distal article (fig. 11, An2).

Mandible: Pars intermedia with two penicils on left and one on right side; bearing few setae; molar penicil composed of three branches; mandibular body slender (fig. 12, Mdl/r).

Maxillula: Medial endite with two weak penicils and apical tip; lateral endite with 4+6 teeth; five of inner set cleft; slender stalk present (fig. 12, Mx1).

Maxilla: Subrectangular with both lobes subequal in width; scattered trichiform setae present; more than ten cusps apically of medial lobe (fig. 12, Mx2).

Maxilliped: Basipodite slender; with sulcus lateralis; palp three-articulate; setal tufts prominent; setae of proximal article subequal in length; endite slender; apically setose; prominent penicil on rostral surface present (fig. 12, Mxp).

Pereopods: Slender; with scattered tricorn-like setae (fig. 13, PE1-7); carpus with prominent antenna-grooming brush; along medial margin covering almost one half of carpus length; ornamental sensory spine with hyaline apex; slightly striate (fig. 13, Sc1); dactylus with simple dactylar seta (fig. 13, Dac); inner claw short; interungual seta with hyaline spatuliform apex. Sexual dimorphism: Male pereopods 1 to 2 with setal brushes on carpus; propus 1 inflated; equipped with prominent setal brush.

Pleopods: Pleopod exopodites rhomboid; with one to two sensory spines laterally; endopodites subtriangular; no respiratory organs discernible in light microscope (fig. 14, PL1-5). Sexual dimorphism: Male pleopod 1 endopodite rounded; endopodite slender; more than two times longer than exopodite; apex acute; slightly bent sidewards; distal third with caudomedial row of spines; laterally with three to five subapical teeth (fig. 14, PL1). Pleopod 2 exopodite pointed; laterally sinuous; endopodite slender; one third longer than exopodite (fig. 14, PL2).

Uropod: As in other species of the genus.

Genital papilla: Ventral shield with straight margins basally; terminal spatula with orifices surpassing ventral shield; slightly bilobate (fig. 14, Gen).

Distribution: Andaman Islands, Grub Island.

Remarks: *Littorophiloscia denticulata* was described from the Andaman Islands as a close relative of *L. albicincta* (Vandel, 1973) and *L. occidentalis* (Ferrara & Taiti, 1983). The outstanding autapomorphy of this species is the denticulated male pleopod 1 endopodite; which is unique among its congeners. On the other hand, the species mentioned above have a pleopod 1 with a similar structure. It is not possible to evaluate the phylogenetic status of this character. Due to the relative simplicity of its structure in comparison to its congeners, like *L. richardsonae* (Holmes and Gay, 1904) and *L. riedlii* (Strouhal, 1966), the latter formerly placed in *Stenophiloscia* (Strouhal, 1966), *L. denticulata* may be close to the basis of this genus.

The occurence of this species in Guatemala most probably is due to human introduction. The locality is 20 km north of Puerto Barrios, the main sea harbour of Guatemala. *L. denticulata* may have been displaced with cargo from the South East Asia, where it is assumed to be autochthonous, because its closest relatives occur in the Indopacific region (Taiti & Ferrara, 1986a) and the radiation of this group might have taken place in this area.

Burmoniscus Collinge, 1914

A diagnosis of *Burmoniscus* was given in Taiti & Ferrara (1986b).

Type species: *Burmoniscus moulmeinus* Collinge, 1914 (senior synonym of *Philoscia coeca* Budde-Lund, 1895).

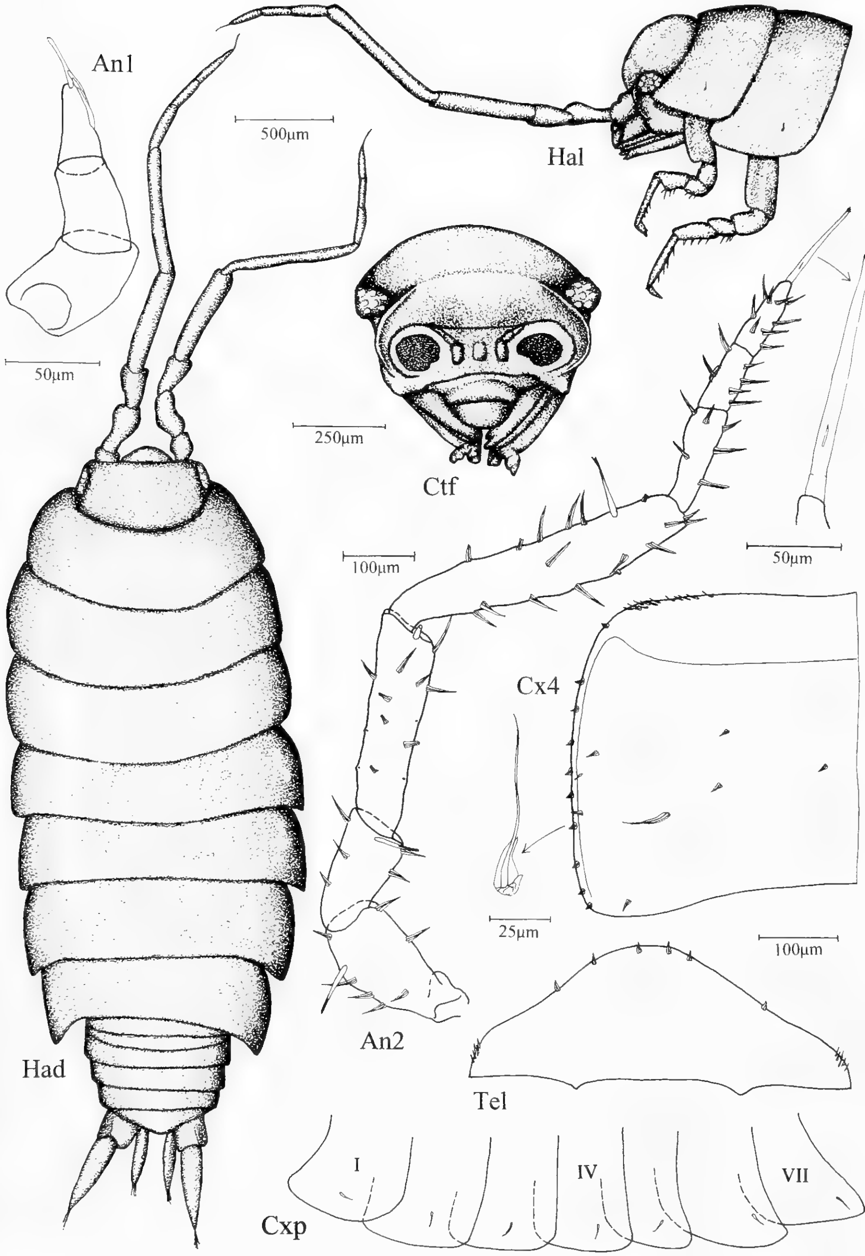

FIG. 11: *Littorophiloscia denticulata* (Ferrara & Taiti, 1981), ♂ 3.5mm body length. An1 antennula; An 2 antenna, with detail of apical organ; Ctf cephalothorax in frontal view; Cx4 coxal plate IV, with detail of nodulus lateralis; Cxp coxal plates with position of noduli laterales; Had habitus in dorsal view; Hal habitus in lateral view; Ste tricorn-like seta of pleotelson; Tel pleotelson.

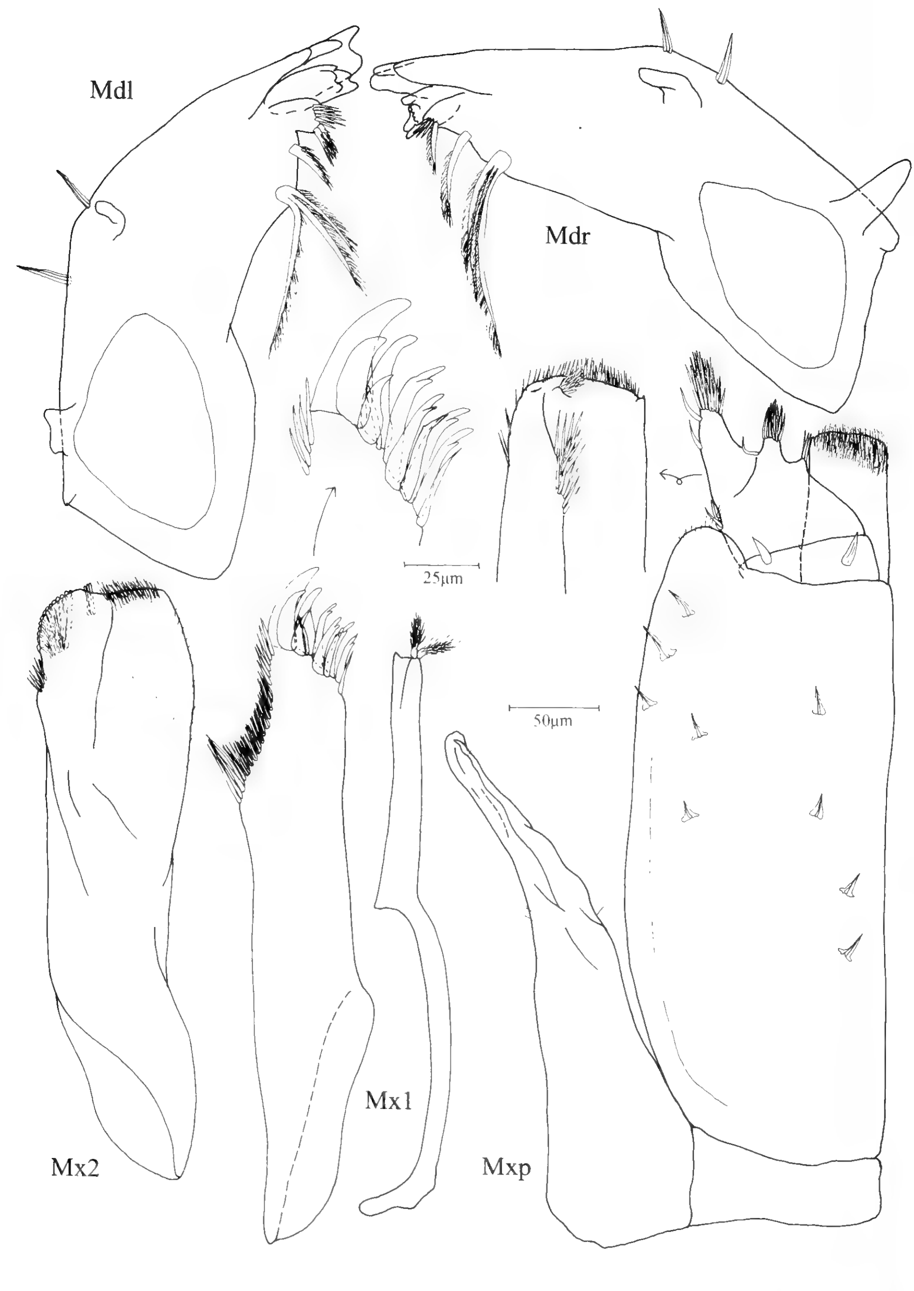

FIG. 12: *Littorophiloscia denticulata* (Ferrara & Taiti, 1981), ♂ 3.5mm body length. Mdl/r left and right mandible; Mxp maxilliped, with detail of endite in rostral view; Mx1 maxillula, with details of apical lateral endite in rostral view; Mx2 maxilla.

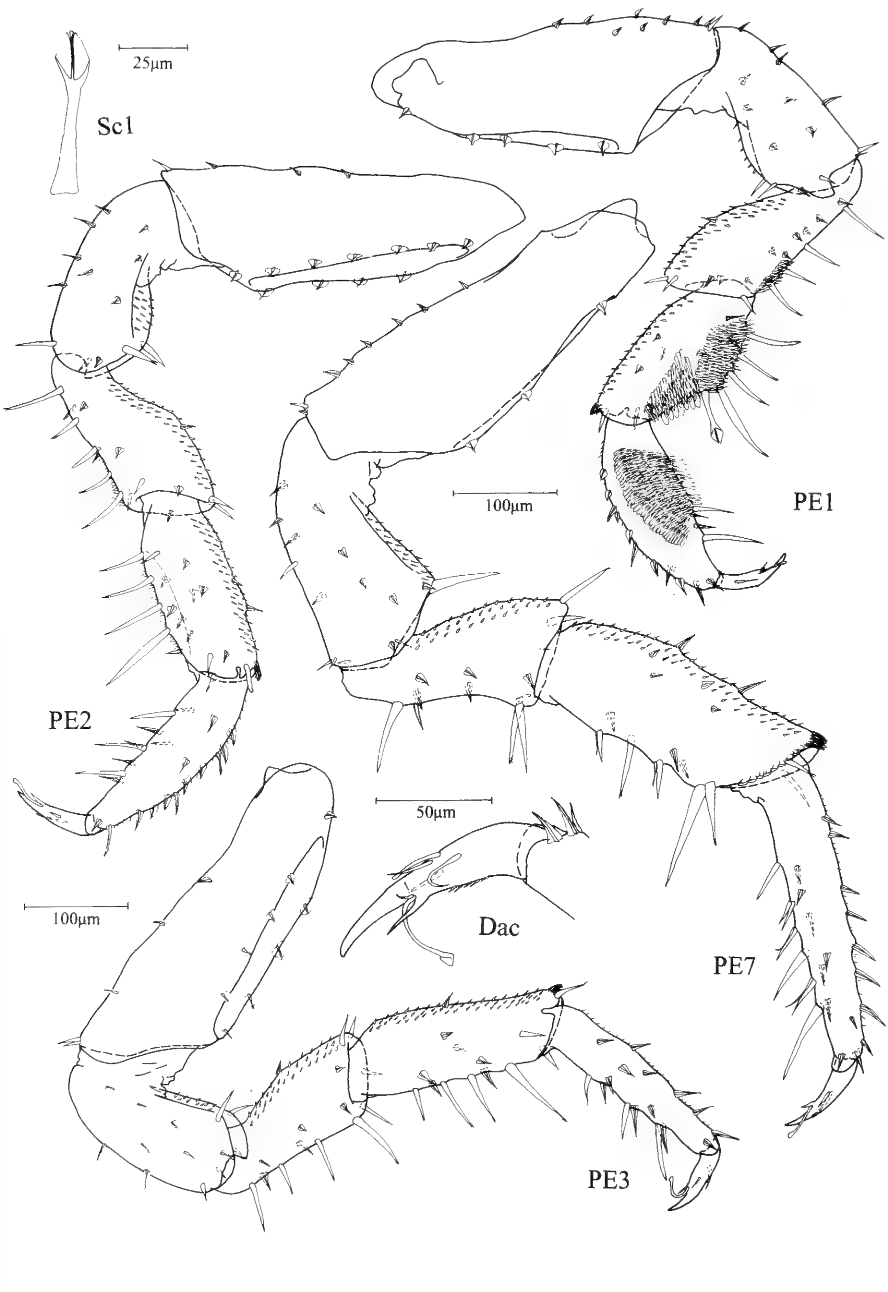

FIG. 13: *Littorophiloscia denticulata* (Ferrara & Taiti, 1981), ♂ 3.5mm body length. Dac dactylus of pereopod 1 in rostral view; PE1-7 pereopods 1 to 7 in caudal or rostral (PE1) view; Sb4 tricorn-like seta of basis 4; Sc1 ornamental sensory spine of carpus 1.

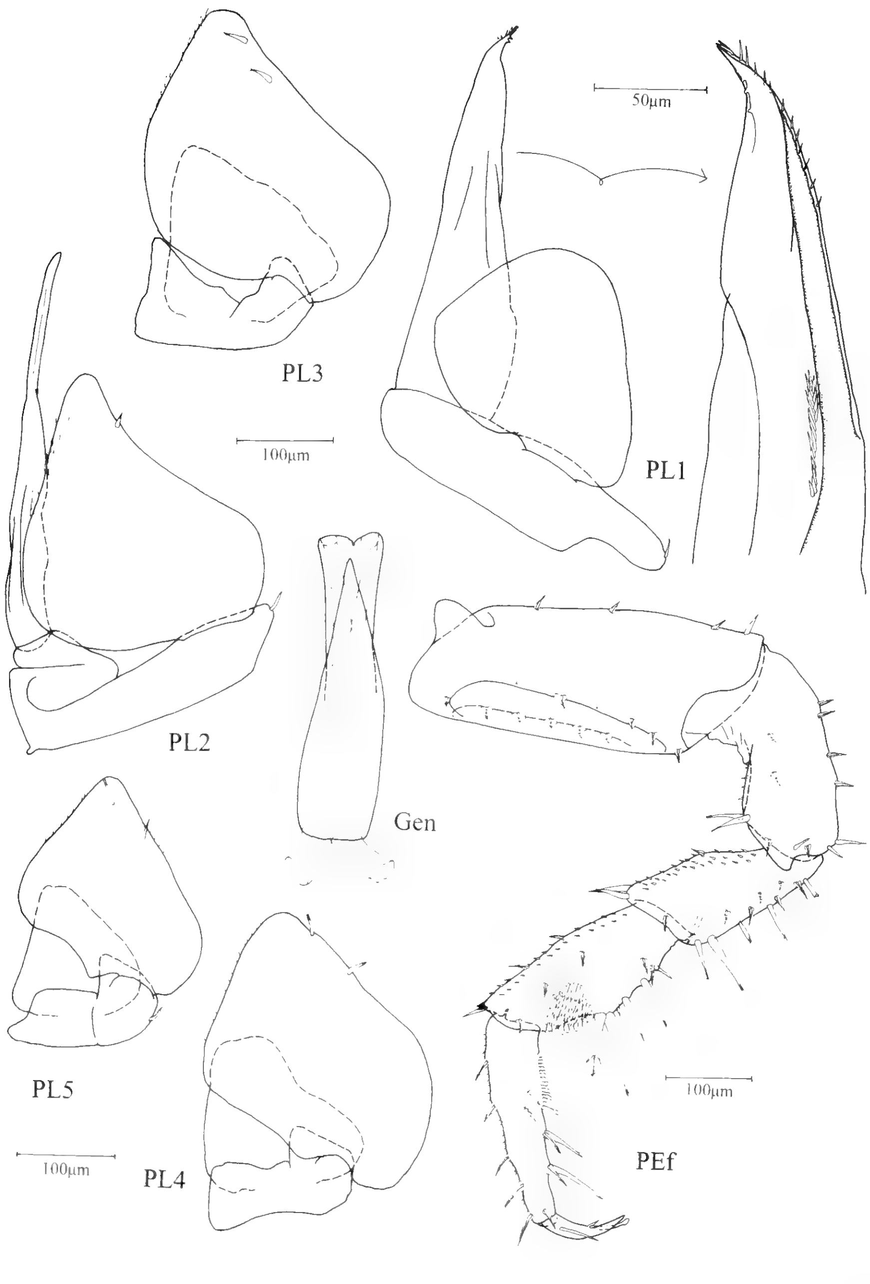

FIG. 14: *Littorophiloscia denticulata* (Ferrara & Taiti, 1981), ♂ 3.5mm body length / ♀ 4.5mm body length. Gen genital papilla; PEf female pereopod 1 in rostral view; PL1-5 pleopods 1 to 5 in rostral view, with detail of endopodite 1 in caudal view.

NUMBER OF NOMINAL SPECIES: 58, two are reported from the Neotropics, both of which most pobably introduced from West Africa and Southeast Asia.

DISTRIBUTION: Southeast Asia, East Africa, West Africa (?); some species with circumtropical distribution due to dispersal by man.

REMARKS: The genus *Burmoniscus* Collinge, 1914 has been revised and newly defined by Taiti & Ferrara (1986b). It is a heterogeneous, probably paraphyletic group, comprising blind and unpigmented species and species which are superficially similar to several members of *Ischioscia* Verhoeff, 1928; e.g., *Burmoniscus davisi* Taiti & Manicastri, 1988. In fact, no autapomorphies of the genus are described until now. The characteristic position of the nodulus lateralis on coxal plate II is shared with, e.g., *Anchiphiloscia* Stebbing; 1908 (Ferrara & Taiti, 1986), from which it differs in the presence of gland pores and a sulcus marginalis, certainly plesiomorphies of *Burmoniscus*.

The genus is distributed in the Oriental region, where it occurs with more than 30 species. The first record from South America was *B. meussii* (Holthuis, 1949), reported from Brazil by Araújo *et al.* (1996). It is found in suitable habitat in Venezuela as well (pers. obs.). Records of the little known species *Burmoniscus kohleri* (Schmalfuss & Ferrara, 1978) are presented from Guatemala for the first time.

Burmoniscus kohleri (Schmalfuss & Ferrara, 1978) Figs 15-18

Rennelloscia kohleri Schmalfuss & Ferrara, 1978

Material examined: 2 ♂ (max.body length 2.5 mm), several ♀: Guatemala, Izabal, Aldea de Los Irrayoles, in scarse leaf litter in a plantation of Blepheridium? guatemalensis (Rubiaceae), leg. A. Leistikow; 17.X.1998, MNHG and author's collection; 2 ♂ (max. body length 2.5 mm); 5 ♀: Guatemala, Izabal, Aldea de Los Irrayoles; in a meadow with Cyperus sp.; leg. 17.X.1998, A. Leistikow, author's collection; 2 ♂; 3 ♀: Guatemala, Izabal, Lívinston, finca in the western part of town on hill, under rotting stems of Cocos palms, leg. A. Leistikow; 21.X.1998; author's collection

Colour: Violaceous brown with light patches in medial line; paramedially and on coxal plates; vertex densely spotted with light patches; pleon uniformly violaceous brown.

Cephalothorax: Vertex slightly arched; compound eyes composed of about five ommatidia; no linea frontalis and lamina frontalis; linea supra-antennalis present (fig. 15, Ctf).

Pereon: Slender; tegument smooth and shiny; scattered tricorn-like setae; coxal plates with sulcus marginalis and nodulus lateralis; noduli of coxal plate II and IV more remote from margin (fig. 15, Cx3/Cxp).

Pleon: Narrower than pereon; no neopleurae visible in dorsal view; pleotelson with sinuous lateral margins; pointed; bearing few tricorn-like setae.

Appendages:

Antennula: Proximal article wide; medial and distal article forming a cone; aesthetascs at top of distal article (fig. 15, An1).

Antenna: Peduncle five-articulate; length ratio from proximal to distal joint 1: 2: 2: 3: 4; flagellum three-articulate with pairs of aesthetascs on medial and distal article; apical organ as long as distal article; with short free sensilla (fig. 15, An2).

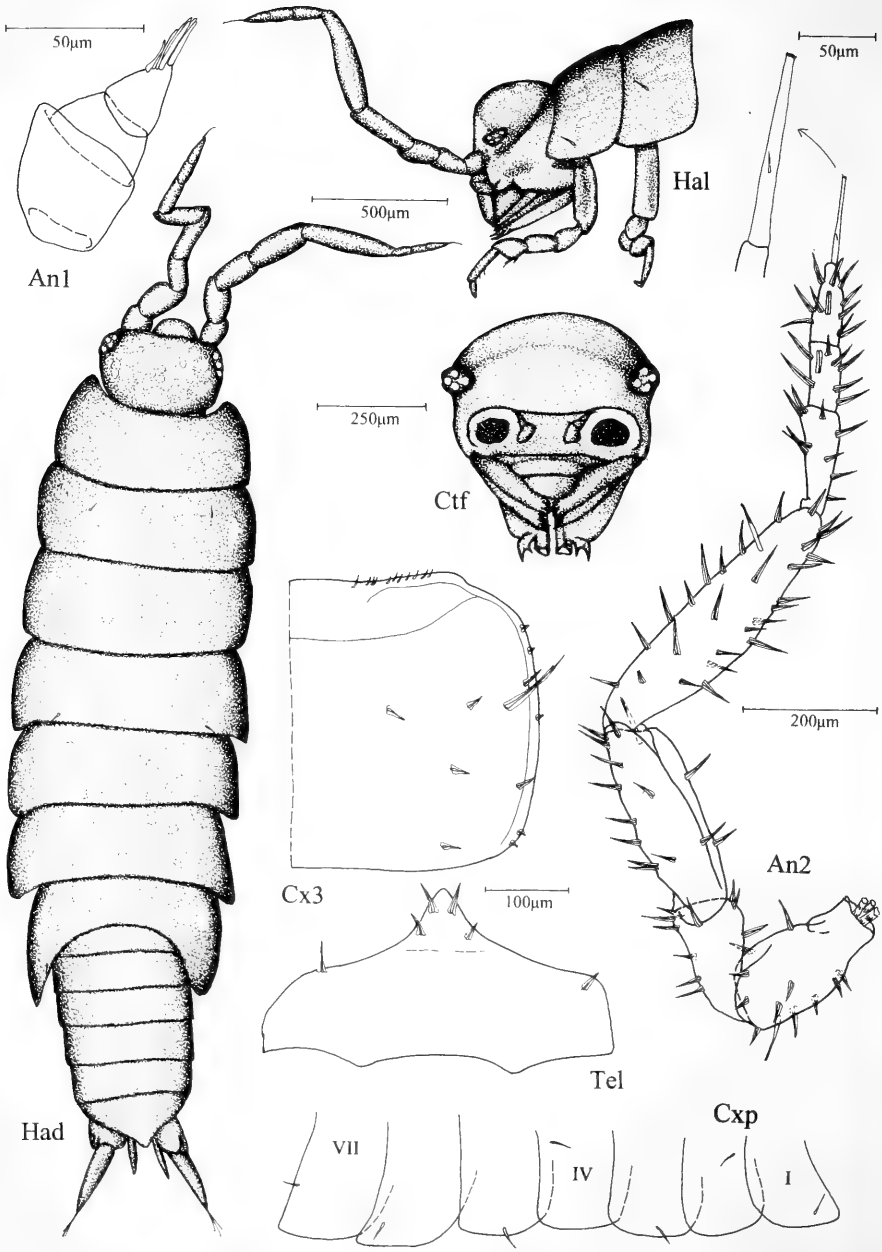

FIG. 15: *Burmoniscus kohleri* (Schmalfuss & Ferrara, 1978), ♂ 2.7mm body length. An1 antennula; An 2 antenna, with detail of apical organ; Ctf cephalothorax in frontal view; Cx3 coxal plate III; Cxp coxal plates with position of noduli laterales; Had habitus in dorsal view; Hal habitus in lateral view; Tel pleotelson.

Mandible: Molar penicil simple; pars intermedia with sparse setation; two penicils on left; one on right side; intermedial penicil present (fig. 16, Mdl/r).

Maxillula: Medial endite pointed; bearing two penicils apically; lateral endite with 4+5 teeth; three of inner set cleft; one double-cleft; one simple (fig. 16, Mx1).

Maxilla: Lateral lobe more than two times broader than medial one; setose; laterally with transverse setal rows; medial lobe with few setae and five apical cusps (fig. 16, Mx2).

Maxilliped: Basipodite with sulcus lateralis; palp with proximal article bearing two setae; inserted close together; distal articles fused; two setal tufts present; proximal one with one prominent seta; endite with strong tooth caudally and knob-like penicil rostrally (fig. 16, Mxp).

Pereopods: Slender with latero-distal setal tuft on carpus (fig. 17, PE1-7); prominent transverse setal brush on rostral surface of carpus 1; half as broad as medial margin; ornamental sensory spine double fringed (fig. 17, Sc1); dactylus with short inner claw (fig. 17, Dac); dactylar seta simple; rather short. No sexual dimorphism discernible.

Pleopods: Pleopod exopodites rhomboid; bearing one to two sensory spines laterally; single row of pectinate scales on caudal surface of exopodite 5; no respiratory areas discernible; endopodites bilobate (fig. 18, PL1-5). Sexual dimorphism: Male pleopod 1 exopodite strongly concave on lateral margin; sinuosity forming almost right angle; endopodite bent laterally; tapering in distal third; medio-caudal row of short spines present (fig. 18, PL1). Pleopod 2 exopodite pointed; laterally sinuous; endopodite slender (fig. 18, PL2).

Uropod: As in other species of the genus.

Genital papilla: Ventral shield stout; slightly surpassed by terminal spatula with orifices (fig. 18, Gen).

Distribution: West Africa, Cameroon.

Remarks: This interesting species was found to be abundant in agricultural areas of the Sierra de las Minas and the Caribbean coast at Lívinston. They live in the leaf litter or in rotten truncs of *Cocos* palms. *B. kohleri* was first discovered in Cameroon, a remarkable location for a member of this genus; since all the other species described are found in East Africa, South Asia and on the islands of the Wallacea. It is possible that this species was also introduced to Cameroon, all the localities where the species was found are close to the coast or to human settlements (Schmalfuss & Ferrara, 1978, 1983 and 1985). Thus, the natural occurence of this species may still be unknown. On the other hand, *Burmoniscus* probably is paraphyletic and *B. kohleri* might not belong to this genus. *B. kohleri* is quite distinct from its congeners due to its minute size of maximally 3 mm and the number of spines along the medial margin of carpus 1 is reduced to two as opposed to three to four spines in other species of *Burmoniscus*.

If this species is native to Cameroon, it is quite isolated from the African Oniscidean fauna by the position of the *noduli laterales* and the simple molar penicil, with one exception: Taiti & Ferrara (1980 and 1982) listed for the West African area a

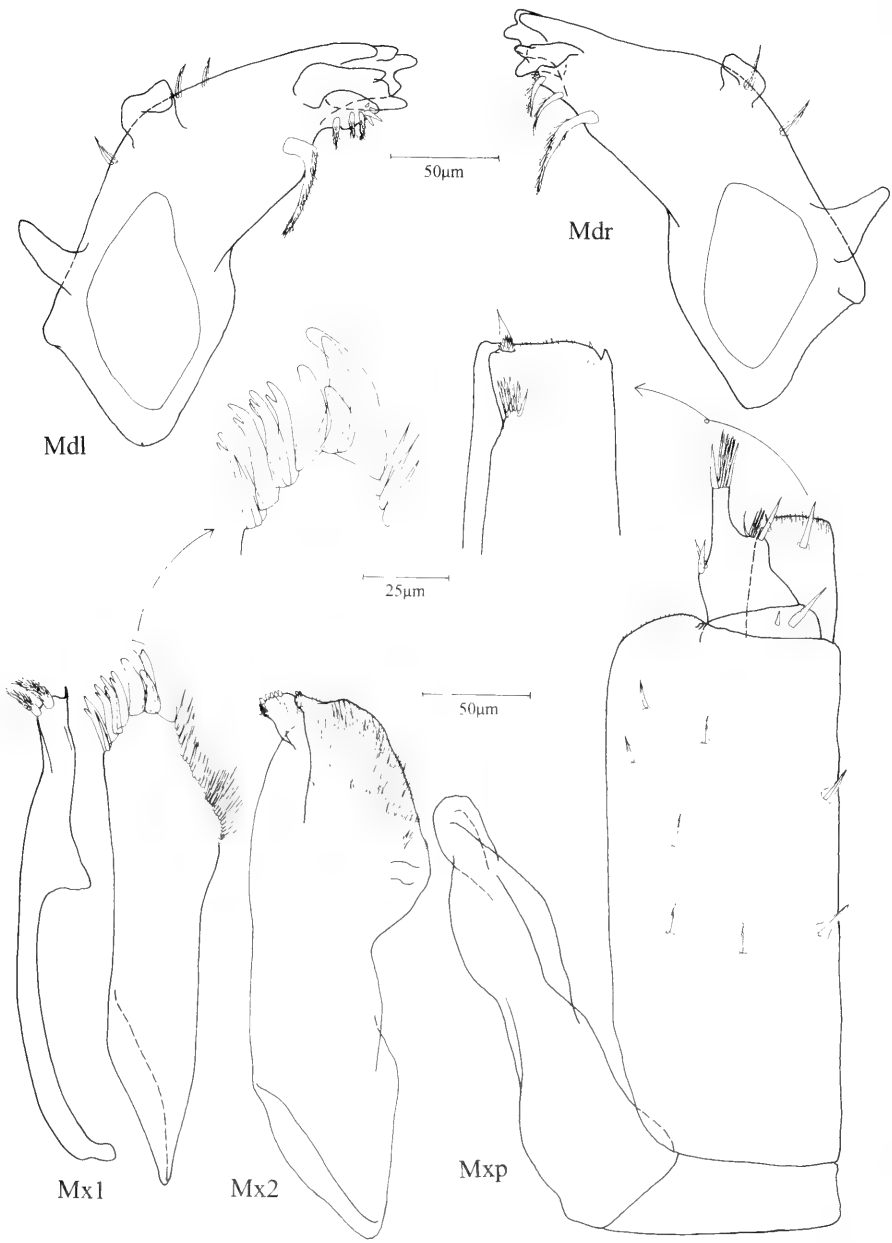

FIG. 16: *Burmoniscus kohleri* (Schmalfuss & Ferrara, 1978), ♂ 2.7mm body length. Mdl/r left and right mandible, with detail of left pars intermedia; Mxp maxilliped, with detail of endite in rostral view; Mx1 maxillula, with detail of apical lateral endite in rostral view; Mx2 maxilla.

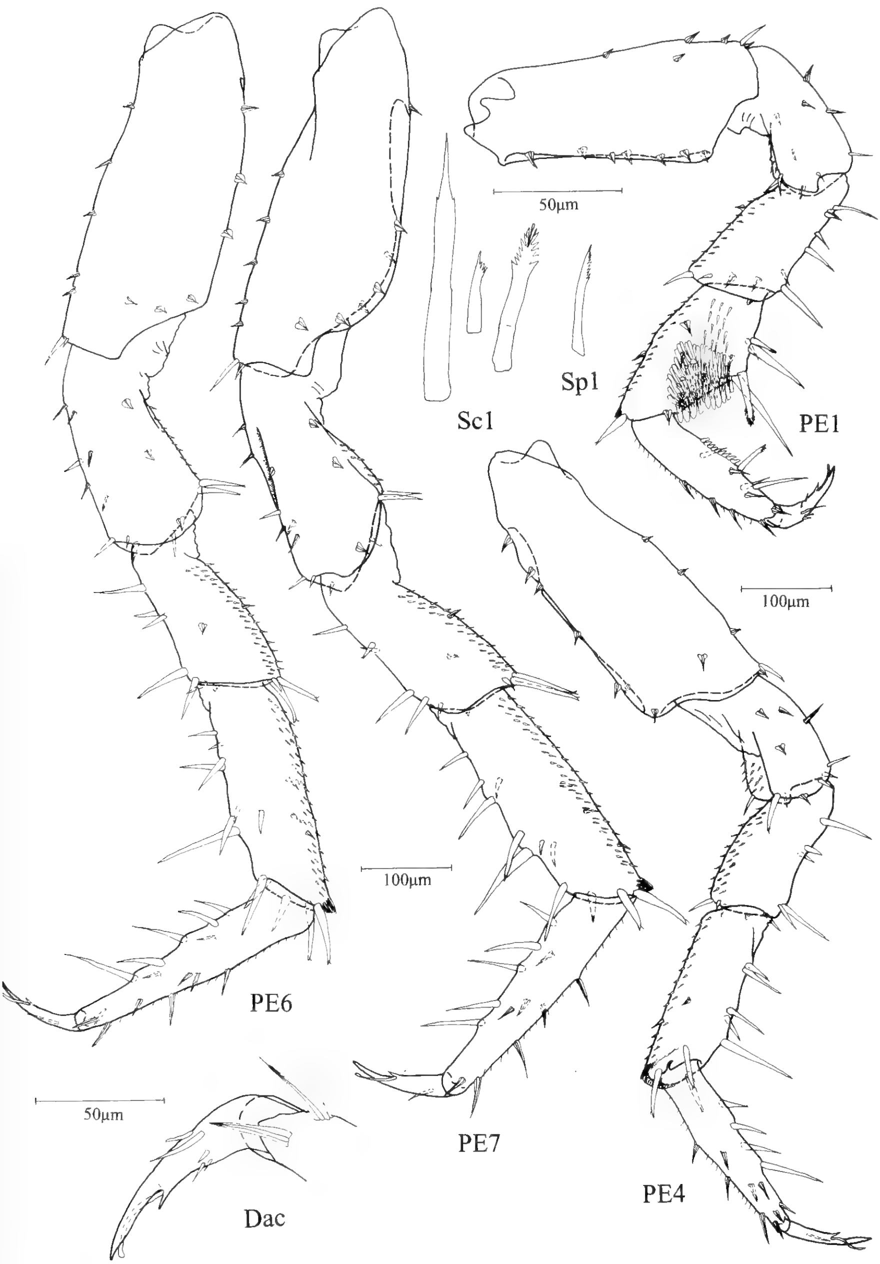

FIG. 17: *Burmoniscus kohleri* (Schmalfuss & Ferrara, 1978), ♂ 2.7mm body length. Dac dactylus of pereopod 7 in rostral view; PE1-7 pereopods 1 to 7 in caudal or rostral (PE1) view; Sc1 ornamental, longest and smallest sensory spines of carpus 1; Sp1 medioproximal sensory spine of propus 1.

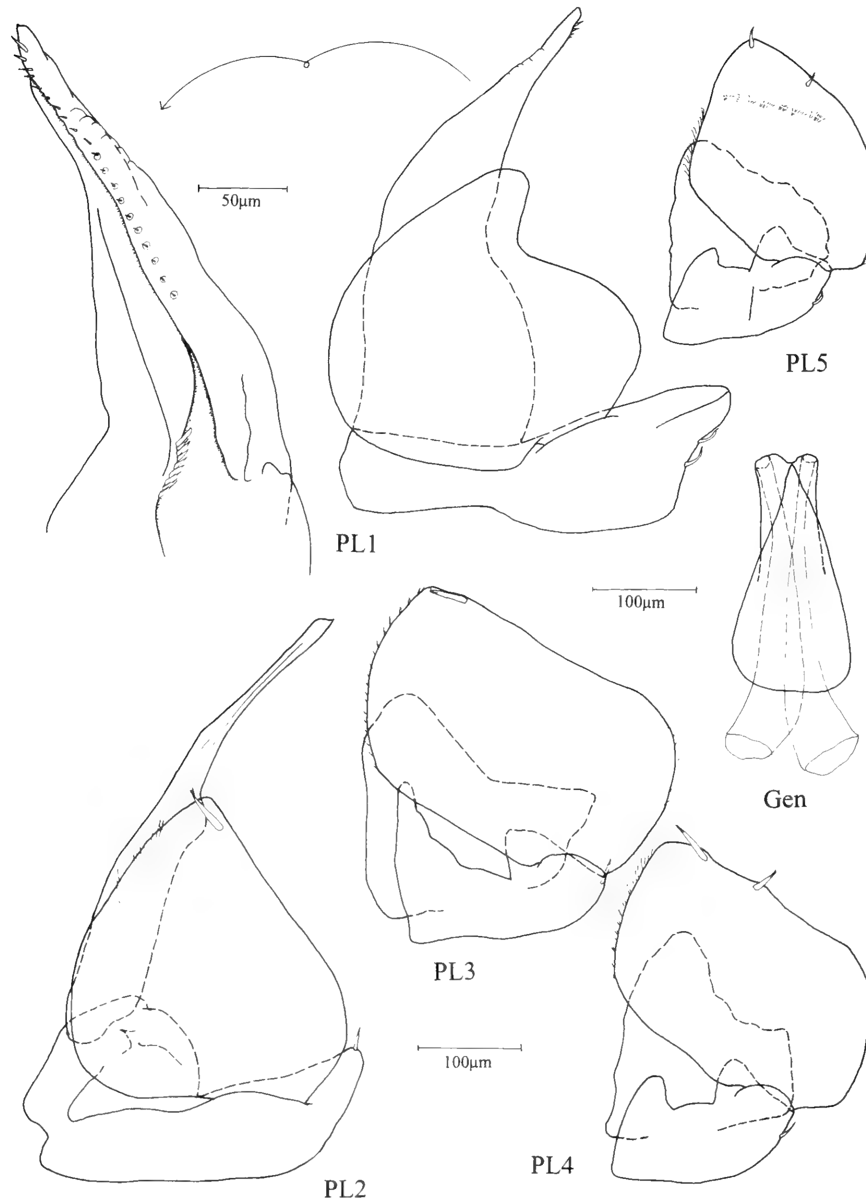

FIG. 18: *Burmoniscus kohleri* (Schmalfuss & Ferrara, 1978), ♂ 2.7mm body length. Gen genital papilla; PL1-5 pleopods 1 to 5 in rostral view, with detail of endopodite 1 in caudal view.

genus which shares these characters. *Zebrascia* Verhoeff, 1942 was described on the basis of a single female of 3 mm body length from Fernando Po (Verhoeff, 1942). This genus now comprises three species; two of them from Cameroon (Schmalfuss & Ferrara, 1978). Interestingly, the pereopod 1 carpus is of similar shape in both *Zebrascia* and *B. kohleri*, and even the number and position of the sensory spines correspond in both taxa. The position of the noduli laterales with respect to the posterior margin of the coxal plates is similar in *Zebrascia* and *B. kohleri* (Schmalfuss & Ferrara, 1978, Taiti & Ferrara, 1986b). It may be well possible that *B. kohleri* belongs to a taxon close to *Zebrascia*; with the following synapomorphies:

- ■ Antenna-grooming brush covering half the medial margin of pereopod carpus 1 [antenna-grooming brush covering less than a third of carpus]
- ■ Sensory spines of carpus 1 arranged in a 2-spine-pattern [sensory spines arranged in a 3-spine pattern]

In the Indopacific species of *Burmoniscus* differ from *B. kohleri* by the pereopod 1 carpus being similar to the relations found in *Androdeloscia* (three-spine-pattern, see below and fig. 20, PE1) and the antenna-grooming brush being not so broad. To clarify this puzzling taxonomic situation, all species of *Burmoniscus* and *Zebrascia* have to be re-examined.

Androdeloscia Leistikow, 1999

REMARK: The genus *Androdeloscia* was recently instituted for the small members of the genus *Prosekia* Vandel, 1968; many species are found in northern South America (Leistikow, 1999), but there are no records from Central America until now. However, two Central American species do belong to this genus, one originally described as a member of *Philoscia* (Mulaik, 1960), the other a new species from Guatemala. Beside *Ischioscia*, *Androdeloscia* is the only genus of Crinocheta of philosciid appearance known to occur in Central America and northern South America (Leistikow, 1997).

Androdeloscia formosa (Mulaik, 1960) Figs 19-22

Synonym: *Philoscia formosa* Mulaik, 1960

Material examined: 1 ♂ (body length 3 mm); 1 ♀: Guatemala, Petén, El Remate, Garden of the Casa de Don David, under coconuts and rotten leaves of *Musa* sp. and different species of deciduous trees, close to pasture at Lake Petén Itza, leg. 27.X.1998, A. Leistikow, author's collection; 3 ♂, several ♀: Guatemala, Petén, causeway between Flores and Sta. Elena, 100 m off Ciudad de Flores; in rotten *Eichhornia* sp. directly at lake shore, leg. 30.X.1998, A. Leistikow; author's collection and MNHG; 5 ♂, 4 ovigerous ♀: Guatemala, Petén, Sta. Elena, road to Grutas Actún Can; 250 m from entrance, under bark of cut trees, leg. 30.X.1998; A. Leistikow, author's collection; 3 ♂, 5 ♀ (Paratypes): Mexico, Tabasco, Palmillas, leg. 18.VIII.1945, F. Bonet, IPNM 1102-E.

Colour: Dorsally purplish brown with pale spots on pereon; medial line dark brown; white central stripe on pereonites I-IV; double line on pereonites V-VII; pleon unmarked.

Cephalothorax: Linea frontalis and lamina frontalis lacking; linea supra-antennalis present; lateral lobes small; compound eyes consisting of eight ommatidia (fig. 19, Ctf).

Pereon: Tegument smooth and shiny; coxal plates without gland pores; sulcus marginalis and noduli laterales present; the latter long and flagelliform; most dorsally inserted on coxal plate IV (fig. 19, Cx3/Cxp).

Pleon: Narrower than pereon; neopleurae of pleonites 3 to 5 small; pleotelson with straight distal margin; bearing some tricorn-like setae.

Appendages:

Antennula: Three-articulate with prominent proximal article; distal joint bulbous; bearing two distinct sets of aesthetascs separated by a shallow depression (fig. 19, An1).

Antenna: Antennal peduncle composed of five articles with length ratio 1: 2: 2: 3: 4; densely covered with tricorn-like setae: flagellum composed of three articles; distal one bearing prominent apical organ; as long as flagellar articles 1 and 2 together (fig. 19, An2).

Mouth parts similar to following species.

Pereopods: Pereopods slender; with setal tuft latero-distally on carpus; carpus 1 with antennal-grooming brush; ornamental sensory spine serrate (fig. 20, Sc1); dactylus with short inner claw and simple dactylar seta; interungual seta straight (fig. 20, Dac). Sexual dimorphism: Male pereopod 7 merus with two small lobes medio-distally; prominent lobe below distal sensory spine, directed distally; covered with small scales (fig. 20, PE1-4; plate 21, PE5-7).

Pleopods: Exopodites rhomboid with two sensory spines laterally; endopodites subrectangular (fig. 22, PL1-5). Sexual dimorphism: Male pleopod 1 exopodite rounded with slight concavity laterally; endopodite rather bulky; basal part containing muscle M49 being half as broad as protopodite; laterally sinuous; distally with prominent hump; apex slightly bent laterally; with short medio-caudal row of spines (fig. 22, PL1). Pleopod 2 exopodite triangular with one sensory spine laterally; endopodite with flagelliform distal half (fig. 22, PL2). Pleopod 5 exopodite with groove for directing pleopod 2 exopodite; apex not elongate (fig. 22, PL5).

Uropod: As in other species of the genus.

Genital papilla: Rather short and slender compared to congeners (fig. 23, Gen).

Remarks: This species belongs to a distinct subtaxon of the genus *Androdeloscia* which is characterised by a sexual dimorphism of the male pereopod 7 merus. It bears several hooks on its medial margin similar to *A. silvatica* (Lemos de Castro & Souza, 1986) and *A. pseudosilvatica* Leistikow, 1999 from the Caribbean region. Particularly *A. pseudosilvatica* resembles *A. formosa*: the male pereopod 7 merus has three hooks and the male pleopod 1 endopodite is bulbous at its base and falciform in the distal part. Both species are separated by several characters. In *A. formosa* the maxillula has a simple tooth more laterally, in *A. pseudosilvatica* the simple tooth is placed medially, the male pereopod 7 merus bears two sensory spines in vicinity of the proximal hook, in *A. pseudosilvatica* there is only one sensory spine, and the male

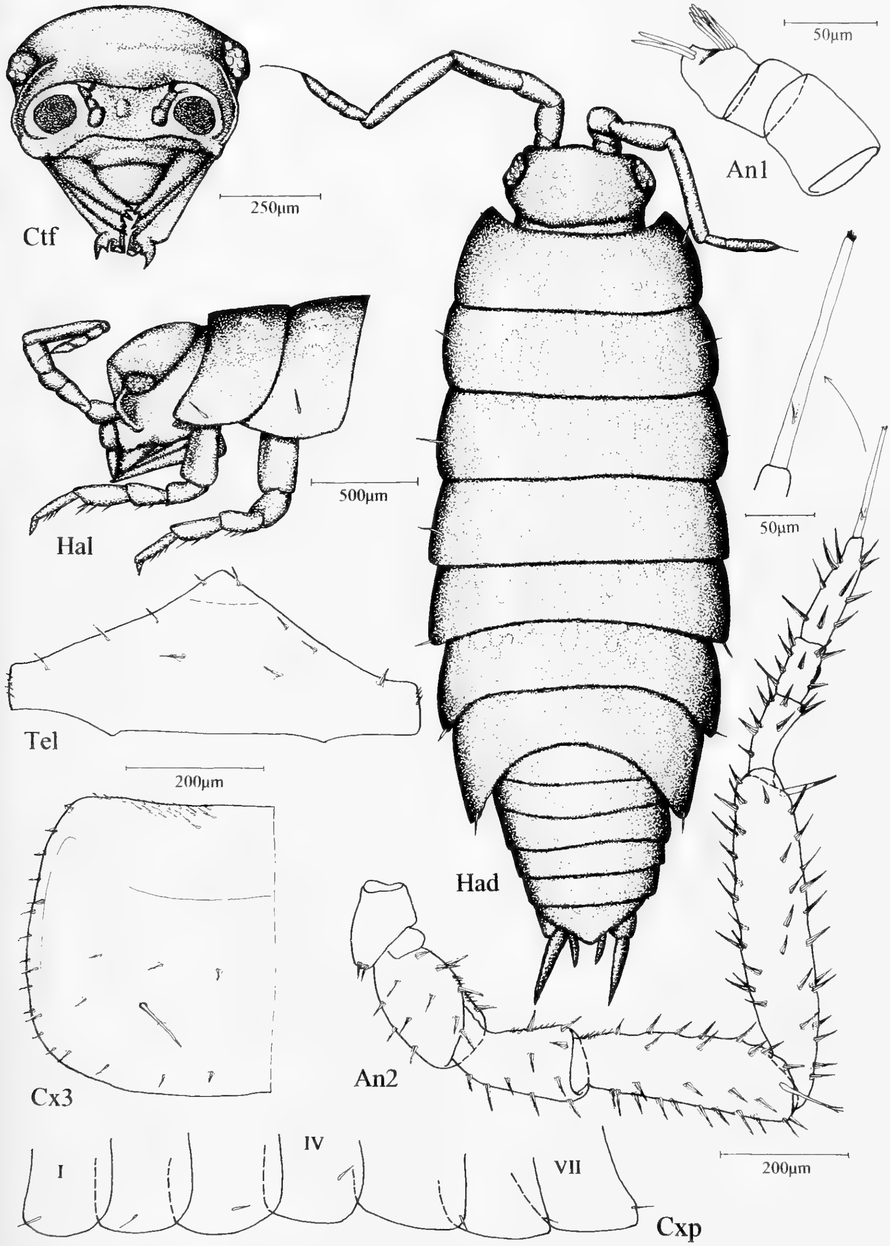

FIG. 19: *Androdeloscia formosa* (Mulaik, 1960), ♂ 4mm body length. An1 antennula; An2 antenna, with detail of apical organ; Ctf cephalothorax in frontal view; Cxp position of noduli laterales on coxal plates; Cx3 coxal plates3; Had habitus in dorsal view; Hal habitus in lateral view; Tel pleotelson.

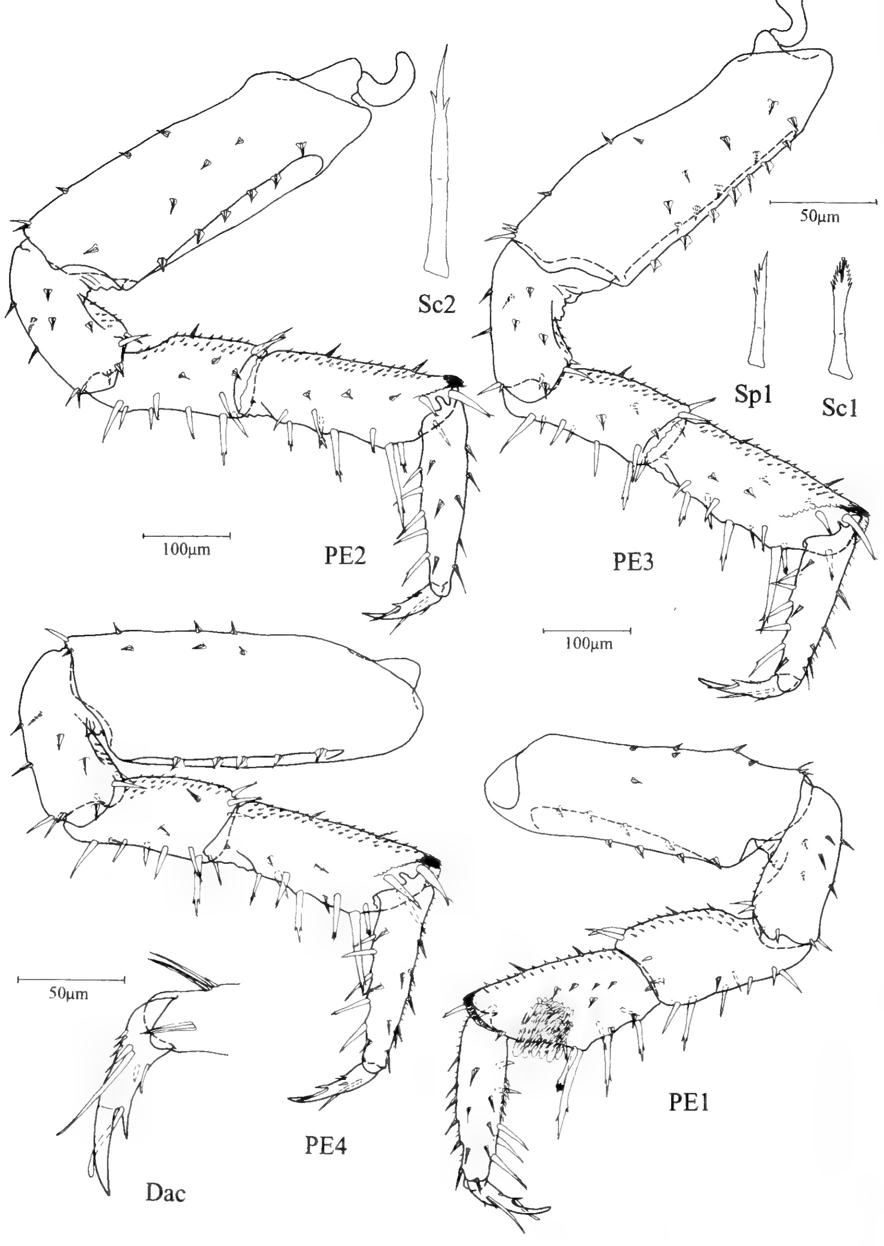

FIG. 20: *Androdeloscia formosa* (Mulaik, 1960), ♂ 4mm body length. Dac dactylus 1 in rostral view; PE1-4 pereopods 1-4 (caudal view), with detail of carpus 1 in rostral view; Sc1 ornamental sensory spine of carpus 1; Sc2 longest sensory spine of carpus 2; Sp1 distal sensory spine of propus 1.

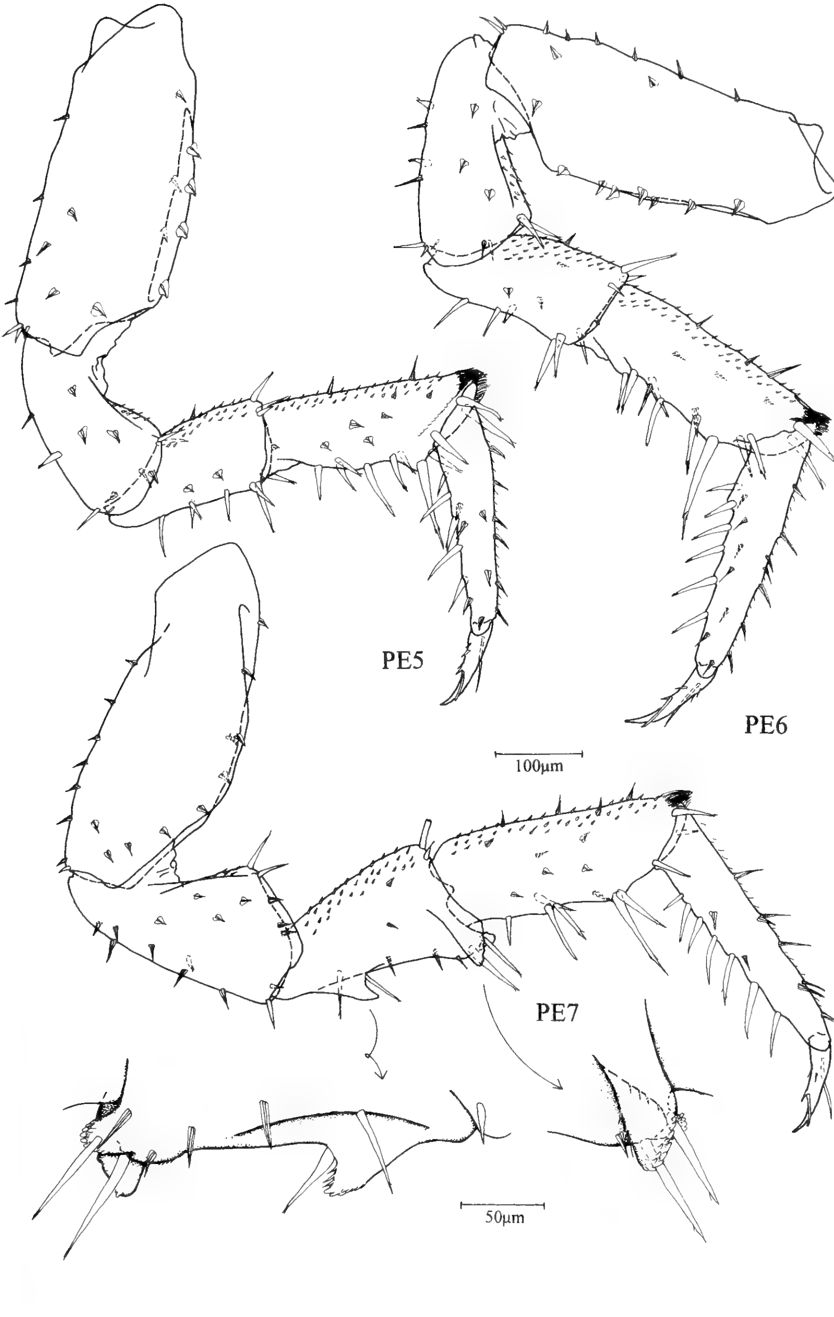

FIG. 21: *Androdeloscia formosa* (Mulaik, 1960), ♂ 4mm body length. PE5-7 pereopods 5-7 in caudal view.

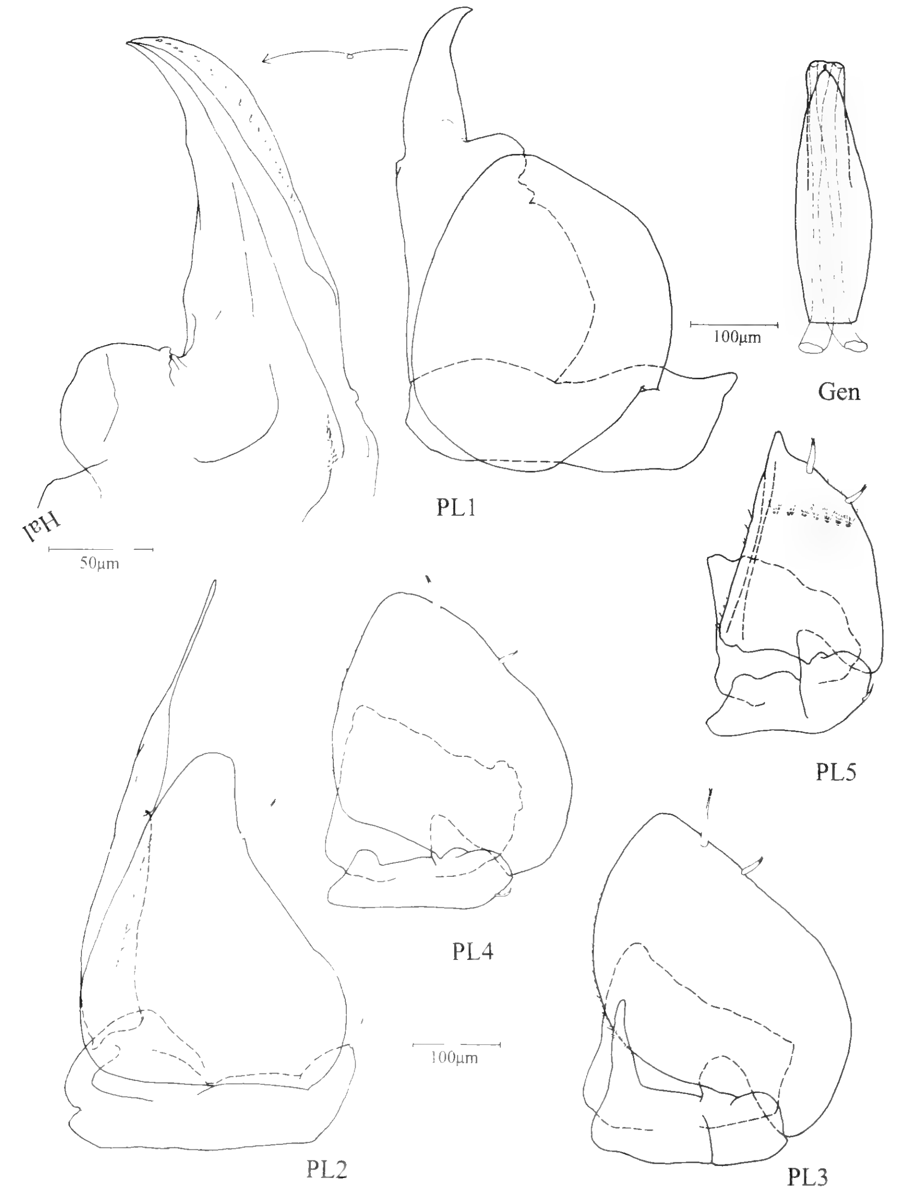

FIG. 22: *Androdeloscia formosa* (Mulaik, 1960), ♂ 4mm body length. Gen genital papilla; PL1-5 pleopods 1-5, rostral view, with detail of endopodite 1 in caudal view.

pleopod 1 endopodite has the apex smooth and a lateral hump on half-length in *A. formosa*, wheras in *A. pseudosilvatica*, the apex bears some lateral hooks and there is no lateral hump. Additionally, the dactylar seta is acute in *A. pseudosilvatica* whereas the apex of the dactylar seta in *A. formosa* is pointed. *A. pseudosilvatica* might be the the adelphotaxon of *A. formosa* and *A. silvatica*, the latter share the lateral hump of the male pleopod 1 endopodite as a synapomorphy.

Androdeloscia valdezi sp. n. Figs 23-26

Material examined: ♂ (holotype, body length 3 mm): Guatemala, Petén, causeway between Flores and Sta. Elena, 100 m off Ciudad de Flores, in rotten *Eichhornia* sp. at lake shore, leg. 30.X.1998, A. Leistikow, MNHG uncatalogised; Paratypes: 3 ♂; several ♀: same data as for holotype, Guatemala, Petén, Sta. Elena, hill facing entrance to Grutas Actún Can, scrubs, loamy soil sparsely covered with leaf litter, leg. 30.X.1998, A. Leistikow, author's collection and UVG; 3 ♂, several ♀: Guatemala; Zacapa, Rio Hondo, north of bridge over Rio Hondo, right bank, in leaf litter, leg. 18.X.1998; A. Leistikow, SMNS.

Diagnosis: Similar to most of its congeners, which do not show sexual dimorphism in the pereopods; differs in the shape of male pleopod 1 endopodite, which is pointed with lateral margin bearing several teeth.

Colour: Mostly as in other species of the genus; dorsally reddish brown with light markings of muscle insertions; cephalothorax heavily spotted.

Cephalothorax: Linea frontalis missing; lamina frontalis weak; linea supra-antennalis prominent; only slightly bent between antennal sockets; lateral lobes small; compound eyes consisting of about eight ommatidia (fig. 23, Ctf).

Pereon: Tegument shiny; dorsum bearing scattered tricorn-like setae; coxal plates with sulcus marginalis and flagelliform noduli laterales; the latter more dorsally inserted on coxal plate IV (fig. 23, Cx3/Cxp).

Pleon: Retracted from pereon; neopleurae attached; pleotelson with straight lateral margin; pointed; bearing short tricorn-like setae.

Appendages:

Antennula: Distal article apically with small tip and two aesthetascs; medially with tuft of about nine aesthetascs; medial article distinctly shorter than proximal one (fig. 23, An1).

Antenna: More slender than in preceding species; especially flagellum; distal article longest; proximal articles subequal in length; apical organ slender, longer than distal article (fig. 23, An2).

Mandible: Molar penicil consisting of a three branches; pars intermedia bearing two penicils on left and one on right mandible; intermedial penicil slender (fig. 24, Mdl/r).

Maxillula: Medial endite similar to preceding species; lateral endite with 4+6 teeth; five of inner set cleft (fig. 24, Mx1).

Maxilla: Lateral lobe only slightly broader than medial lobe; bearing pectinate scales; medial lobe sparsely covered with trichia; apically cuspidate (fig. 24, Mx2).

Maxilliped: As in other species of *Androdeloscia*; basipodite in examined specimen broken (fig. 24, Mxp).

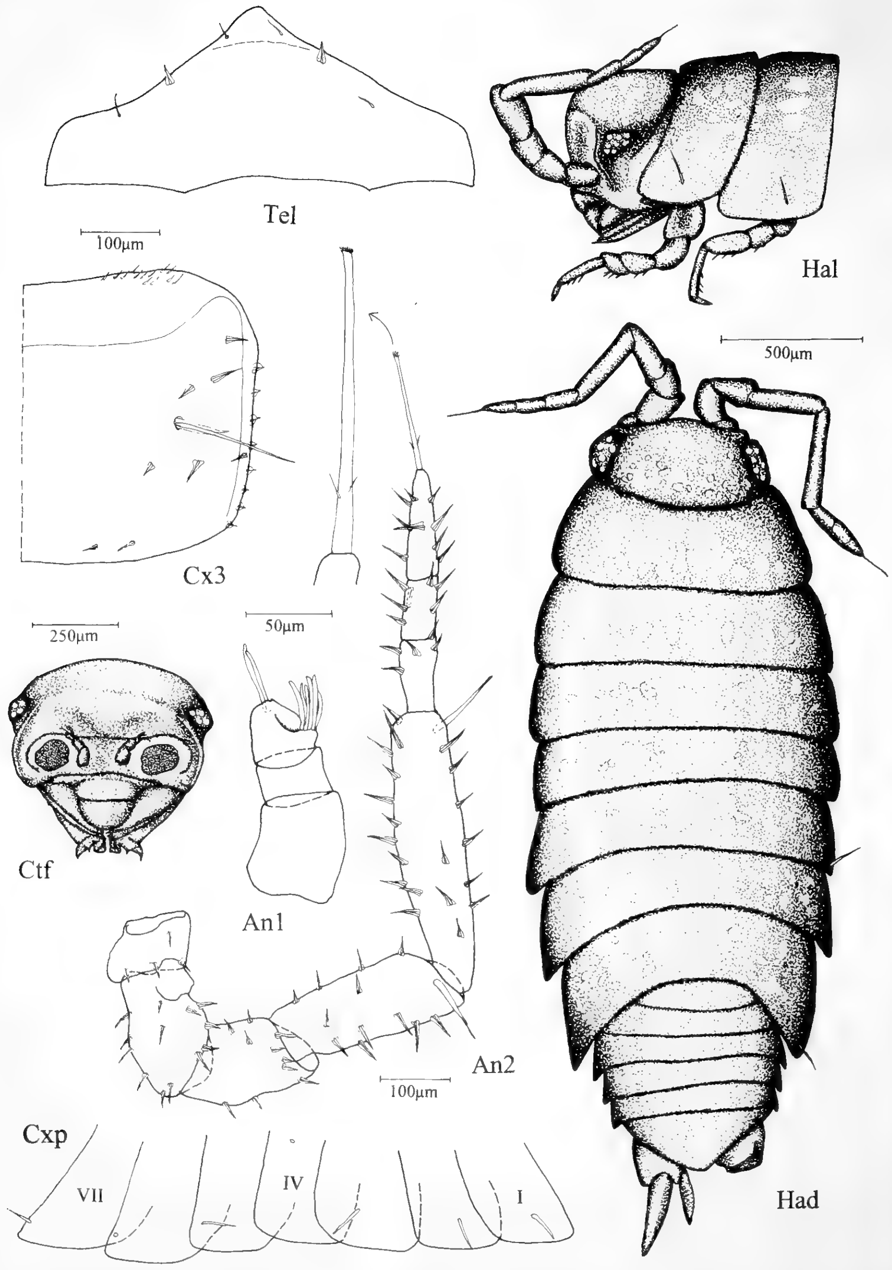

FIG. 23: *Androdeloscia valdezi* sp. n., holotype ♂ 3.5mm body length. An1 antennula; An2 antenna, with detail of apical organ; Ctf cephalothorax in frontal view; Cxp position of noduli laterales on coxal plates; Cx3 coxal plate III; Had habitus in dorsal view; Hal habitus in lateral view; Tel pleotelson.

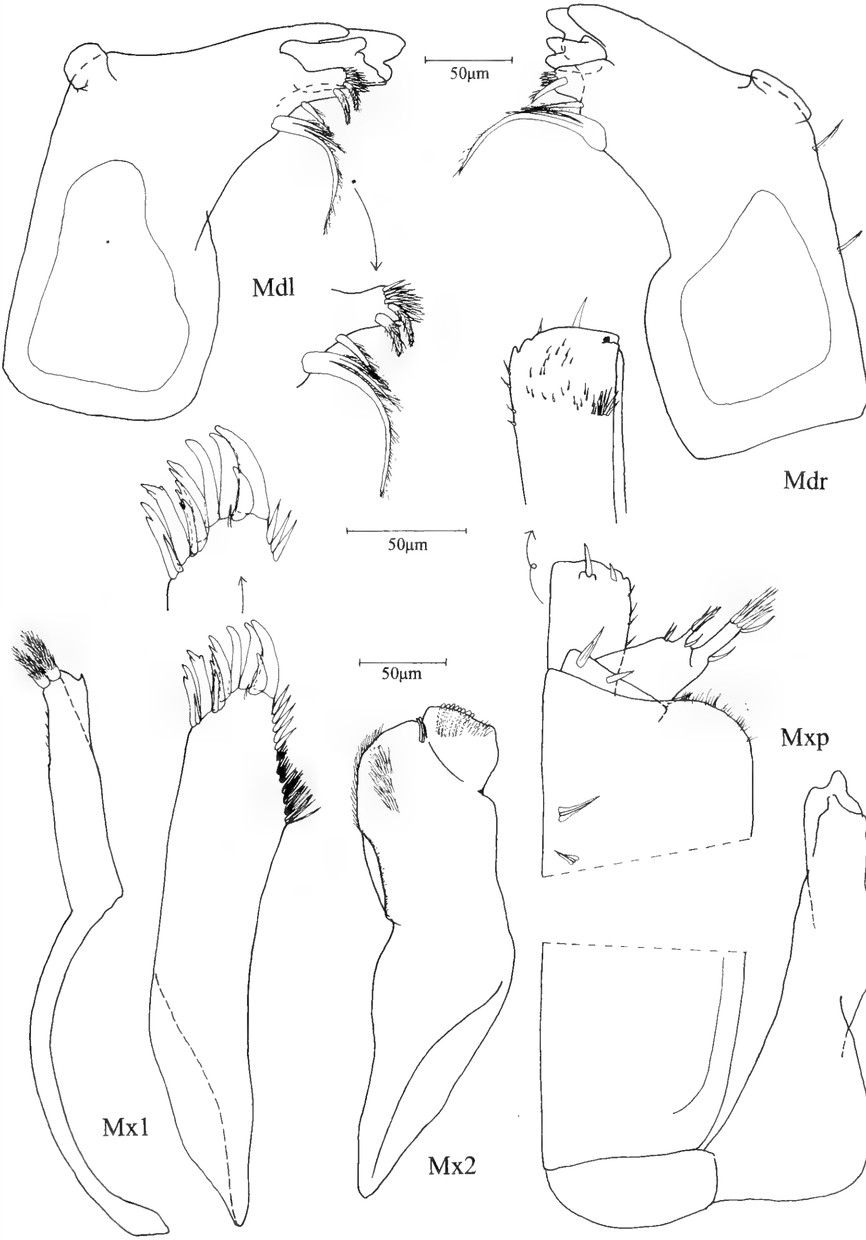

FIG. 24: *Androdeloscia valdezi* sp.n., holotype ♂ 3.5mm body length. Mdl/r left and right mandible, with detail of pars intermedia; Mxp maxilliped, with detail of endite in rostral view; Mx1 maxillula, with detail of apex of lateral endite; Mx2 maxilla.

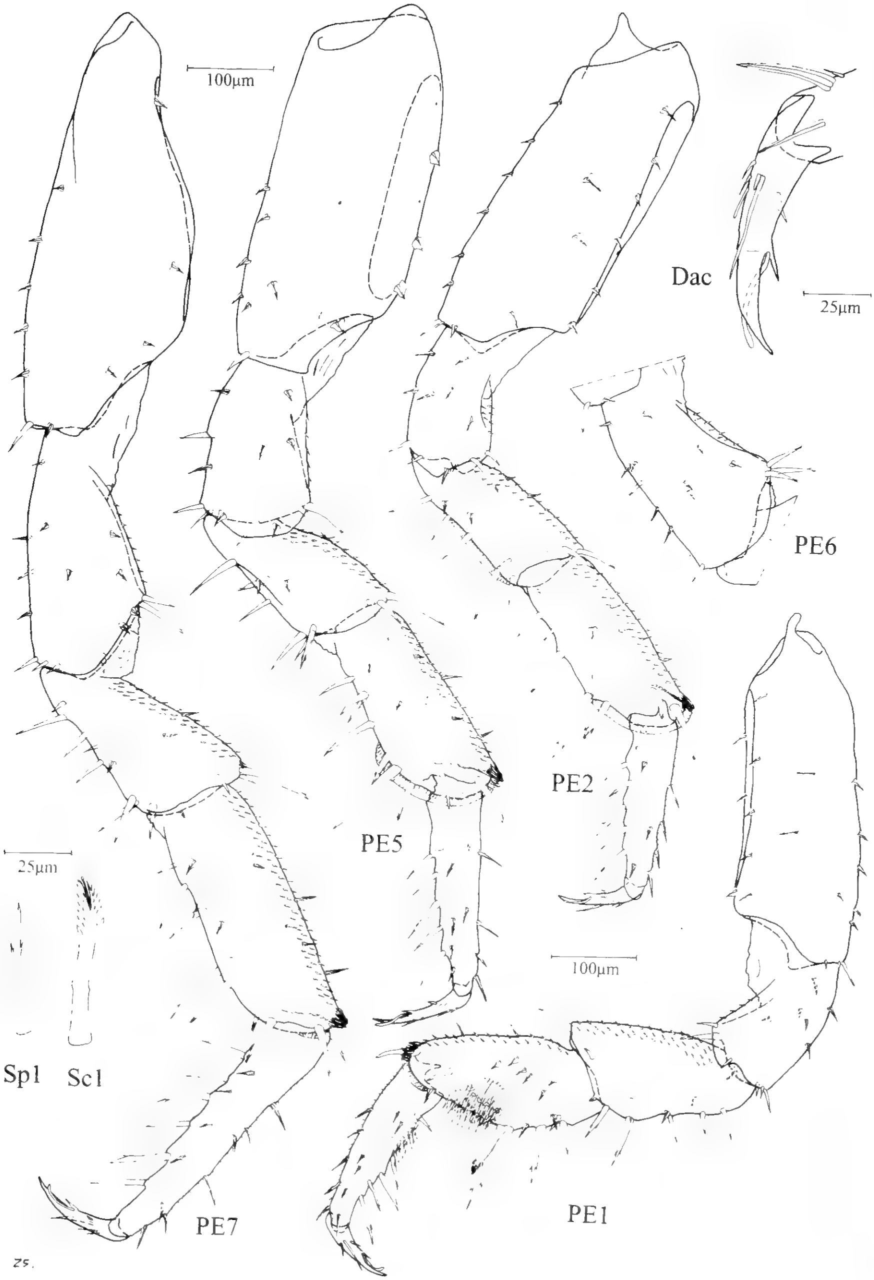

FIG. 25: *Androdeloscia valdezi* sp. n., holotype ♂ 3.5mm. Dac dactylus 1 in rostral view; PE1-7 pereopods 1 to 7 (caudal view), with details of carpus 1 in rostral and ischium 6 in caudal view; Sc1 ornamental sensory spine of carpus 1; Sp1 distal sensory spine of propus 1.

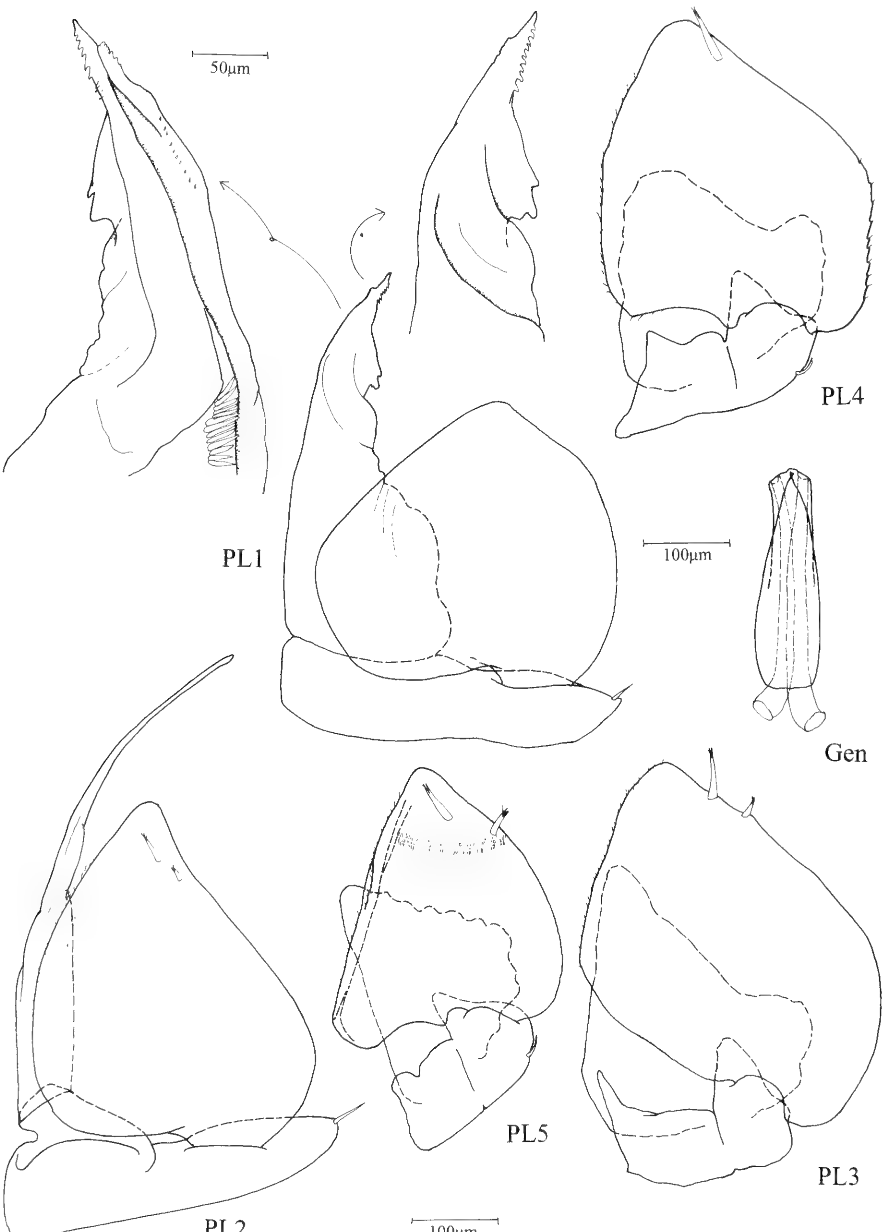

FIG. 26: *Androdeloscia valdezi* sp. n., holotype ♂ 3.5mm body length. Gen genital papilla; PL1-5 pleopods 1-5, rostral view, with details of endopodite 1 in caudal and rostral view.

Pereopods: Rather slender; especially pereopod 1; carpus with antenna-grooming brush and serrate ornamental sensory spine (fig. 25, Sc1); pereopod 2 merus with hyaline fringe medially; dactylus with long inner claw and simple dactylar seta (fig. 25, Dac). Sexual dimorphism not evident (fig. 25, PE1-7).

Pleopods: Pleopod exopodites 3 and 4 elongate rhomboid with two sensory spines laterally; exopodite 5 more or less triangular; endopodites bilobate; no respiratory areas discernible in light microscope (fig. 26, PL1-5). Sexual dimorphism: Male pleopod 1 exopodite rounded; endopodite pointed with lateral margin bearing several teeth; basal part with muscle M49 less than half the length of endopodite; short caudal row of sensory spines (fig. 26, PL1). Pleopod 2 and 5 similar to preceding species (fig. 27, PL2/5).

Uropod: As in other species of the genus.

Genital papilla: Similar to preceding species (fig. 26, Gen).

REMARKS: The new species is close to the "species-group D" of the genus *Androdeloscia* with the autapomorphies: hyaline lobes on the male pleopod 1 endopodite reduced; maxillipedal basipodite slender, apically subrectangular (Leistikow, 1999). The exact systematic position within this group is difficult to access: the male pleopod 1 endopodite in *A. valdezi* is similar to that of *A. conipus* Leistikow, 1999 and related species, but this similarity is possibly a symplesiomorphy. *A. poeppigi* Leistikow, 1999 and *A. malleus* Leistikow, 1999 form the sister group of *A. conipus* and related species. The former have the more derived endopodites 1 within species-group D. The caudo-medial row of spines is reduced and there are two subapical lobes, synapomorphic characters of *A. poeppigi* and *A. malleus*. For the time being, the systematic positon of the new species remains open to debate.

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Euphalerus clitoriae sp. n., a new psyllid species from *Clitoria fairchildiana* (Fabaceae, Papilionoideae), and notes on other *Euphalerus* spp. (Hemiptera, Psylloidea)

Daniel BURCKHARDT[1] & Mariângela GUAJARA[2]
[1] Naturhistorisches Museum, Augustinergasse 2, CH-4001 Basel, Switzerland.
E-mail: daniel.burckhardt@unibas.ch
[2] Universidade Federal Rural do Rio de Janeiro, CPG em Fitotecnia
Seropédica, RJ – 23.851-970, Brazil.
E-mail: guajara@ufrrj.br

***Euphalerus clitoriae* sp. n., a new psyllid species from *Clitoria fairchildiana* (Fabaceae, Papilionoideae), and notes on other *Euphalerus* spp. (Hemiptera, Psylloidea).** - *Euphalerus clitoriae* sp. n. from Brazil, a species developing under waxy filamentous secretions on the leaves of *Clitoria fairchildiana*, is described and illustrated. Its biology is briefly outlined and compared to that of its closest relatives, viz. *E. nidicola* from Peru and *E. maya* from Belize. Differences to these two species are discussed. Based on the study of types, the genitalia of *E. nidicola*, *E. antillensis* and *E. ostreoides* are illustrated completing their insufficient original descriptions.

Key-words: Psylloidea - Fabaceae - Brazil - taxonomy - biology.

INTRODUCTION

The hemipterous jumping plant-lice or psylloids are usually highly host specific and thus a potentially suitable taxon for coevolutionary studies on insect – plant relationships (Burckhardt & Basset, 2000). The necessary taxonomic and phylogenetic base is, however, often insufficient or completely lacking. The genus *Euphalerus* is a good example. It was erected for the Carribean species *E. nidifex* whose larvae form lerps or "nests", i.e. waxy coverings, on Fish poison Bark or Jamaican dogwood (*Piscidia piscipula* and *Piscidia carthegenensis*, Fabaceae, Papilionoideae, Tephrosieae) (Schwarz, 1904; Russell, 1971). Subsequently, a series of mostly tropical New and Old World species were referred to the genus making it extremely artificial. According to Hollis & Martin (1997), the New World species forming lerps or galls on the leaves of Fabaceae make up true *Euphalerus* (Psyllidae, Euphalerinae). The other New World species, associated with *Ceanothus* (Rhamnaceae) and *Cerocarpus* (Rosaceae), are unrelated and belong to the Arytaininae/Psyllinae (Psyllidae) complex. The Old World species, finally, are probably referable to the euphalerine genera *Colophorina* Capener and *Euryconus* Aulmann.

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Twenty two species are currently known in *Euphalerus* s. str. The vast majority is associated with *Lonchocarpus* (Papilionoideae, Tephrosieae). One species is each on *Pithecellobium* (Mimosoideae, Ingeae), *Erythrina* (Papilionoideae, Phaseoleae) and *Piscidia* (Papilionoideae, Tephrosieae) respectively, two species have unknown and one doubtful (*Karwinskia*, Rhamnaceae) host records. Nineteen species are recorded from Central America with one species extending to Florida, and only three are also or exclusively known from South America (Brazil 2, Peru 1) (Hollis & Martin, 1997).

The present paper describes a new species from Brazil developing on *Clitoria fairchildiana* (Papilionoideae, Phaseoleae). The new species broadens the known host range of *Euphalerus*, and suggests that the genus may be more diverse in tropical South America than currently estimated. It is closely related to the gall-forming *E. nidicola* Tuthill from Peru whose larvae are covered in waxy secretions, and the lerp-inhabiting *E. maya* Hollis & Martin from Belize. Hollis & Martin (1997) provided detailed descriptions of the species attacking *Lochocarpus* in Belize. Here we give illustrations of the male and female genitalia of *E. antillensis* Caldwell & Martorell and *E. nidicola* Tuthill, and of the male genitalia of *E. ostreoides* Crawford whose original descriptions lack sufficient detail and which were not treated by Hollis & Martin (1997).

MATERIAL AND METHODS

The morphological terminology follows Hollis (1976) and Hollis & Martin (1997). Measurements and some drawings were made from slide mounted material. The drawings for *E. antillensis* and *E. nidicola* were made from temporary mounts in glycerine.

Material is cited from following institutions: Naturhistorisches Museum Basel, Switzerland - NHMB; Angelo Moreira da Costa Lima Entomological Collection, Seropédica, Brazil - CLEC; Natural History Museum, London, UK - BMNH; United States National Museum of Natural History, Washington, DC, USA (psylloid collection in USDA, Beltsville, MD) - USNM; Muséum d'histoire naturelle, Geneva, Switzerland - MHNG.

TAXONOMIC TREATMENT

Euphalerus clitoriae sp. n. Figs 1-3, 13, 16-23

Holotype ♂, Brazil: State of Rio de Janeiro, Campus and residential area of the Universidade Federal Rural do Rio de Janeiro, Seropédica, 22°44' S 43°43' W, 9.ix.1999, *Clitoria fairchildiana* (M. Guajará), dry mounted (NHMB).

Paratypes, Brazil: 20 ♂, 20 ♀, 10 larvae or larval skins, same data as holotype, dry mounted (NHMB, CLEC, BMNH, USNM, MHNG); 6 ♂, 6 ♀, 4 larvae, same data but 30.v. 1999, dry and slide mounted (NHMB, CLEC, BMNH).

Material not included in type series. Brazil, many adults and some larvae, same data as holotype but 30.v.1999 and 9.ix.1999, preserved in 70 % alcohol (NHMB).

Adult. Body dirty greyish white with small blackish dots, in mature specimens thorax dorsally, abdomen and genitalia dark. Antennal segments 1-8 light with dark apices, segments 9 and 10 entirely dark. Forewing membrane transparent, colourless, with blackish dots as in fig. 16, middle of cells very weakly infuscate; veins whitish with black dots. Legs whitish with dark dots, tarsi blackish.

Small species (see measurements below). Genal processes longer than vertex along mid-line, conical, subacute apically (fig. 17). Antenna 1.97-2.13 times as long as head width, segment 3 (1.32 times) longer than segment 8. Ultimate two rostral segments 0.41-0.43 times as long as head width. Forewing (fig. 16) 2.24-2.31 times as long as wide, 3.67-3.93 times as long as head width; pterostigma moderately long, 0.5 times as long as vein Rs; surface spinules leaving broad spinule-free stripes along the veins; reduced in basal half of cell r_1 and r_2, occupying only a small area in cell c+sc. Metatibia 0.93-0.97 times as long as head width, bearing a small basal spine and an incomplete crown of apical spurs.

Male proctiger (fig. 1) bulbous, lacking lateral lobes. Paramere in profile (fig. 2) with each an anterior and a posterior lobe. Distal portion of aedeagus (fig. 3) hook-shaped; apex of terminal tube of ductus ejaculatorius truncate.

Female proctiger (fig. 13) more or less evenly tapering, dorsal margin weakly concave, apex narrowly rounded; 1.00 times as long as head width, 3.21 times as long as circumanal ring, 1.56 times as long as subgenital plate.

Measurements in mm (1 ♂, 1 ♀). Head width 0.63; antenna length 1.25-1.35; forewing length 2.33-2.50; male proctiger length 0.26; paramere length 0.23; length of distal segment of aedeagus 0.23; female proctiger length 0.63.

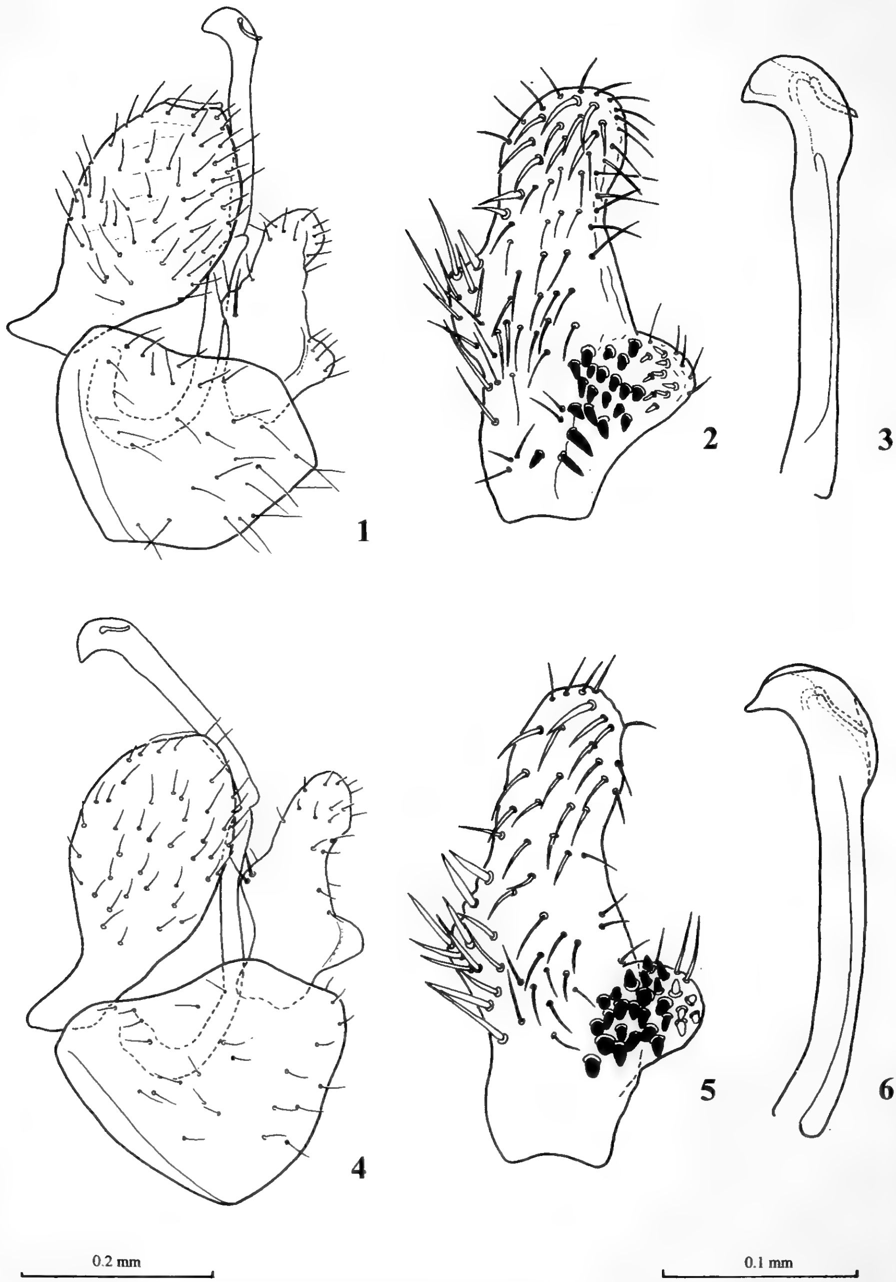
Fifth instar larva (fig. 18). Antenna 8-segmented with one rhinarium on each of segments 3, 5, 7 and 8. Tibiatarsus of foreleg with one large apical and one smaller subapical spur (fig. 19); tibiotarsi of mid and hindlegs with one large and two small spurs. Subgenital plate with two apical processes bearing three teeth each (fig. 20).

Host plant. Clitoria fairchildiana Howard (= *racemosa*) (Fabaceae).

Biology. The eggs are laid along the veins of the leaves. The larvae sit on the leaves and stems hidden under white coverings consisting of waxy hair-like filaments (fig. 21). There is no sign of deformations on the leaves (fig. 22). When the larval density is high, the leaves turn yellow and drop. Strongly infested trees can loose all their leaves (fig. 23).

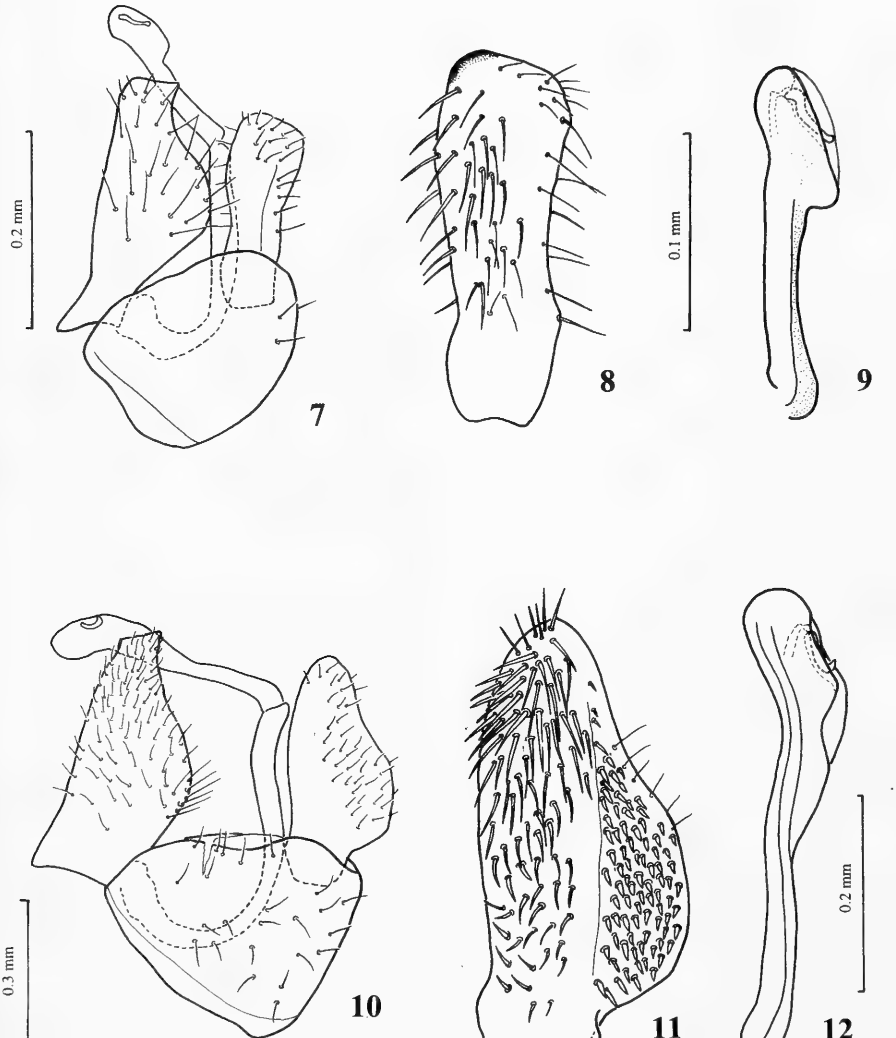
Comments. E. clitoriae, which is a member of the *E. ostreoides* species group as defined by Hollis & Martin (1997), is closely related to *E. nidicola* Tuthill, 1959 from Peru, and *E. maya* Hollis & Martin, 1987 from Belize based on following characters. Small sized *Euphalerus* spp.; head with long, conical genal processes; antenna longer than 1.5 times head width; forewing clear, bearing dark spots lacking transverse bands; metatibia with a small basal spine and an incomplete crown of apical spurs; male proctiger bulbous without lateral lobes; paramere complex, irregularly S-shaped with a group of long thick setae in the middle of the foremargin and a group of heavily sclerotised peg setae on the inner surface of the posterior lobe; female subgenital plate, in profile, with angular ventral margin.

E. clitoriae differs from *E. maya* in the slightly larger body dimensions, the longer antenna, the shorter pterostigma of the forewing, the details in the genital structure and the apex of the larval caudal plate which has three points on each tubercle instead of two. *E. clitoriae* is differentiated from *E. nidicola* by the much more expanded, almost black body coloration, which is orange to light brownish in *E. nidicola*, the blackish dots on the forewings which are brown in *E. nidicola*, the shorter



FIGS 1-6

Euphalerus spp. 1, 4: Male genitalia, in profile; 2, 5: paramere, inner face; 3, 6: distal portion of aedeagus. 1-3: *E. clitoriae* sp. n.; 4-6: *E. nidicola* Tuthill. Scale lines: figs 1, 4 = 0.2 mm, figs 2, 3, 4, 6 = 0.1 mm.



FIGS 7-12

Euphalerus spp. 7, 10: Male genitalia, in profile; 8, 11: paramere, inner face; 9, 12: distal portion of aedeagus. 7-9: *E. antillensis* Caldwell & Martorell; 10-12: *E. ostreoides* Crawford. Scale lines: fig. 7 = 0.2 mm, figs 8, 9 = 0.1 mm, fig. 10 = 0.3 mm, figs 11, 12 = 0.2 mm.

antenna, the more reduced fields of surface spinules in the forewing, the details of the genitalia (for *E. nidicola* see figs 4-6, 14); the female proctiger is slightly shorter and apically more thickened in *E. clitoriae* but longer and apically pointed in *E. nidicola*.

The three species differ also in their geographical and host plant ranges. The larval biology of *E. clitoriae* is intermediate. It shares with *E. nidicola* waxy filamen-

tous coverings but differs by not causing depressions on the leaves. This character is as in *E. maya* which is characterised by the production of a lerp.

Euphalerus antillensis **Caldwell & Martorell** Figs 7-9, 15

Euphalerus antillensis Caldwell & Martorell, 1951: 612. Holotype ♂, Puerto Rico: Guànica, on the Guànica - Guánica Central Road, in front of stone quarry, 28.viii.1947, breeding abundantly on the undersides of the leaves of "geno-geno", *Lonchocarpus domingensis* (Caldwell & Martorell) (USNM).

Material examined. Puerto Rico: 1 ♂, 1 ♀ paratypes, same data as holotype (USNM).

Adult. Member of the *nidifex* species group (as defined by Hollis & Martin, 1997). Metatibia with a small basal spine and grouped apical spurs.

Male proctiger (fig. 7) with narrow lateral lobes. Paramere in profile (fig. 8) lamellar, obliquely truncate apically, inner surface covered in long setae. Distal portion of aedeagus (fig. 9) with oval apical dilatation, rounded apically; apex of terminal tube of ductus ejaculatorius rounded.

Female proctiger (fig. 15) strongly tapering to the middle, digitiform in apical half, dorsal margin strongly concave, apex narrowly rounded.

Euphalerus nidicola **Tuthill** Figs 4-6, 14

Euphalerus nidicola Tuthill, 1959: 6. Holotype ♂, Peru: few km below La Merced, 1.i.1947, on "oropel", *Erythrina* sp. (Tuthill) (USNM).

Material examined. Peru: holotype ♂, allotype ♀, 1 ♂, 1 ♀ paratypes (USNM).

Adult. Member of the *ostreoides* species group (as defined by Hollis & Martin, 1997).

Male proctiger (fig. 4) bulbous, lacking lateral lobes. Paramere in profile (fig. 5) with each an anterior and a posterior lobe. Distal portion of aedeagus (fig. 6) hook-shaped; apex of terminal tube of ductus ejaculatorius truncate.

Female proctiger (fig. 14) irregularly tapering, dorsal margin weakly but distinctly concave, apex subacute.

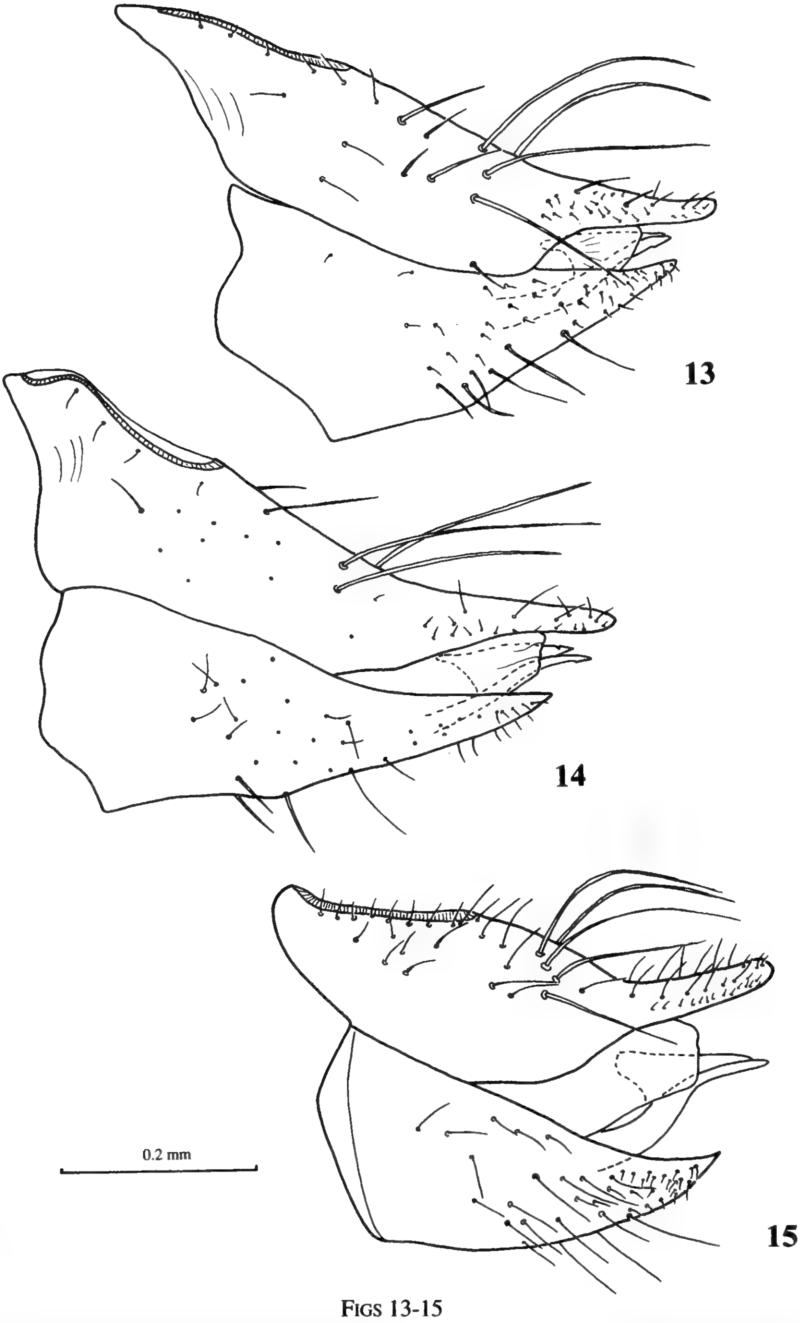
Fifth instar larva. Tuthill (1959) mentioned the presence of many larvae. In the collection of the USNM we could, however, find only the adult types.

Euphalerus ostreoides **Crawford** Figs 10-12

Psyllid, Tavares, 1920: 124; 1922: plate 19 figs 3-5. Galls on the leaves of an undetermined species of Leguminosae (Timbó), Brazil: Rio de Janeiro State, Nova Friburgo; Rio de Janeiro State, surroundings of Rio de Janeiro; São Paulo State, Itu; between Rio Vermelho and the city of Bahia.
Euphalerus ostreoides Crawford, 1925: 62. Syntypes 2 ♂, 1 ♀, Brazil: São Paulo, Itu, making very peculiar galls on the leaves of an undetermined species of Leguminosae (Tavares) (USNM).
Costa Lima, 1942: 107; Silva *et al.*, 1968: 201; Russell, 1971: 10; Hollis & Martin, 1997: 241.

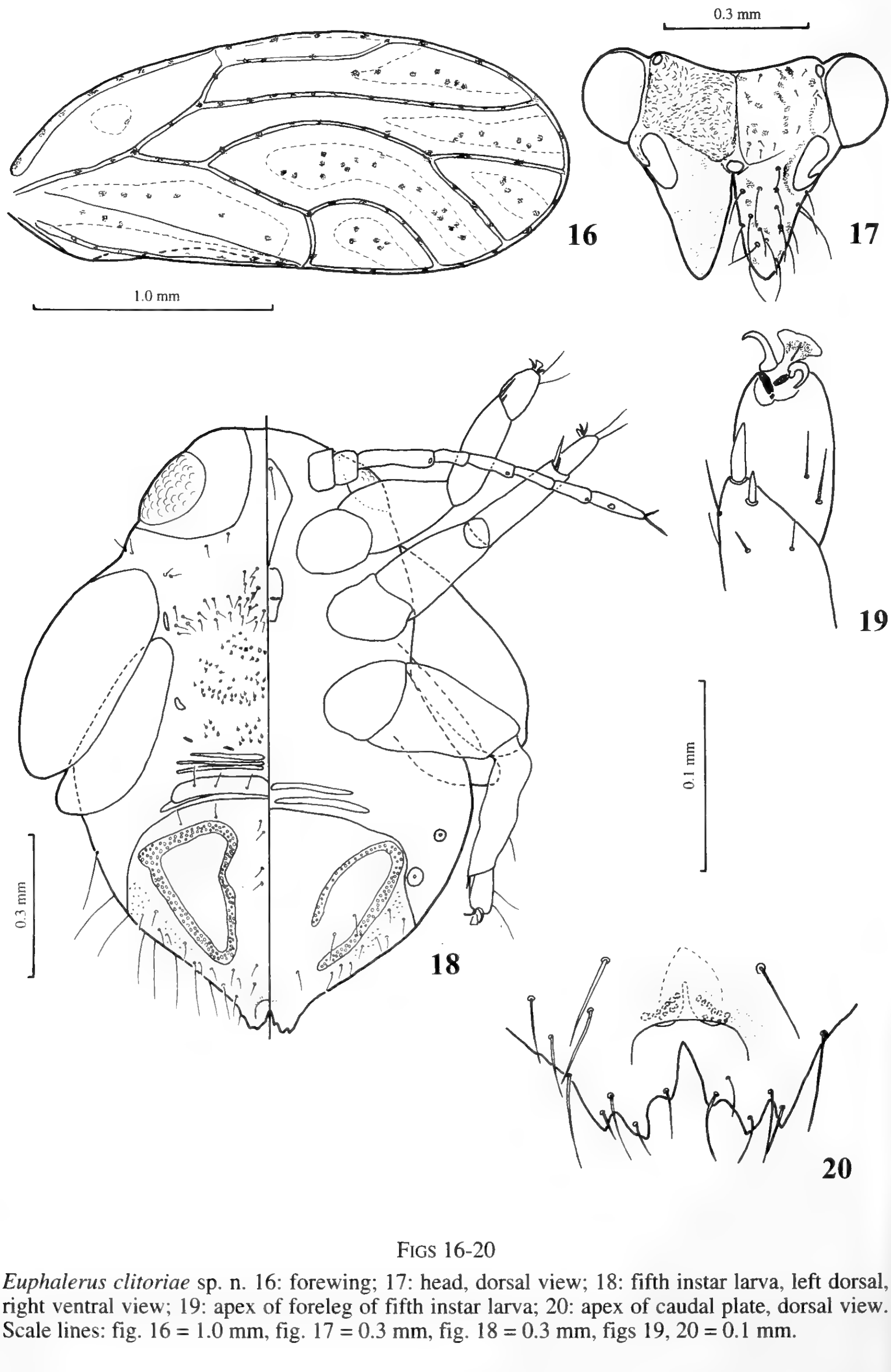
Material examined. Brazil: syntype ♂, São Paulo, Itu, (Tavares) (slide mounted, USNM).

Adult. Member of the *ostreoides* species group (as defined by Hollis & Martin, 1997). Large species (see measurements below). Genal processes shorter than vertex along mid-line, broadly rounded apically. Antenna 2.32 times as long as head width, segment 3 about as long as segment 8. Ultimate two rostral segments 0.39 times as long



FIGS 13-15

Euphalerus spp., female genitalia, in profile. 13: *E. clitoriae* sp. n.; 14: *E. nidicola* Tuthill; 15: *E. antillensis* Caldwell & Martorell. Scale line = 0.2 mm.



FIGS 16-20

Euphalerus clitoriae sp. n. 16: forewing; 17: head, dorsal view; 18: fifth instar larva, left dorsal, right ventral view; 19: apex of foreleg of fifth instar larva; 20: apex of caudal plate, dorsal view. Scale lines: fig. 16 = 1.0 mm, fig. 17 = 0.3 mm, fig. 18 = 0.3 mm, figs 19, 20 = 0.1 mm.

FIG. 21. White waxy hair-like secretions by the larvae of *Euphalerus clitoriae* sp. n. on *Clitoria fairchildiana* leaves and stems.

FIG. 22. Wax covered larvae of *Euphalerus clitoriae* sp. n. on *Clitoria fairchildiana* leaves lacking pit-like deformations.

FIG. 23. Tree of *Clitoria fairchildiana* with almost no leaves due to heavy infestion of *Euphalerus clitoriae* sp. n.

as head width. Forewing 2.34 times as long as wide, 3.06 times as long as head width; pterostigma relatively short, 2.6 times as long as vein Rs; surface spinules present in apical part of all cells except for c+sc, leaving broad spinule-free stripes along the veins; radular spinules covering broad triangular patches along the wing margin in cells r_1, r_2, m_1, m_2 and cu_1. Metatibia 0.77 times as long as head width, bearing a conspicuous basal spine and an incomplete crown of apical spurs.

Male proctiger (fig. 10) with distinct lateral lobes. Paramere in profile (fig. 11) with a large posterior lobe, inner face with an anterior field of longer, more spaced setae and a posterior field with peg-like, densely spaced setae. Distal portion of aedeagus (fig. 12) rounded apically, with inflated apical half; apex of terminal tube of ductus ejaculatorius truncate.

Female unavailable.

Measurements in mm (1 ♂). Head width 1.15; antenna length 2.68; forewing length 3.54; male proctiger length 0.47; paramere length 0.47; length of distal segment of aedeagus 0.47.

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Zur Biologie des "Eingeweidefisches" *Carapus acus* (Brünnich, 1768) (Carapidae, Teleostei), mit Hinweisen auf eine nicht-parasitische Ernährung[1]

Kerstin KLOSS und Wolfgang PFEIFFER
Zoologisches Institut der Universität Tübingen
Auf der Morgenstelle 28, D-72076 Tübingen,
und
Laboratoire Arago, Université Paris VI
F - 66650 Banyuls-sur-mer.

On the biology of the pearlfish *Carapus acus* (Brünnich, 1768) (Carapidae, Teleostei), with indications of a non-parasitic nutrition. - 450 *Stichopus regalis* (Cuvier), caught with a trawl-net at a depth of 70-110 m off Banyuls-sur-mer (France) contained 38 *Carapus acus*. We found only two pearlfish in 85 *Holothuria tubulosa* Gmelin caught in less than 10 m of seawater. We kept pearlfish in aquaria and analysed their behaviour by means of computer analysis of video records. The manner by which the fish enter their hosts was studied (see summary). In the wild most specimens of *C. acus* are found in *S. regalis*, yet in our aquaria *C. acus* only entered *H. tubulosa* if they could choose between both species. We studied the stomach contents of *C. acus* and found crustaceans. The stomachs examined did not contain any holothurian tissue. Our results give reason to agree with Emery (1880), who stated that *C. acus* is an inquiline, to whom the host holothurian serves as a shelter only.

Key-words: pearlfish - *Carapus acus* - Carapidae - Teleostei - host holothurian - *Stichopus regalis* - *Holothuria tubulosa* - stomach contents - behaviour - parasitism - inquilinism.

EINLEITUNG

Der "Eingeweidefisch" *Carapus acus* (Brünnich, 1768) (gängiges Synonym *Fierasfer acus*) ist in jeder Beziehung außergewöhnlich und erregte aufgrund seiner besonderen epidermalen Kolbenzellen bereits 1957 die Aufmerksamkeit des Zweit-Autors (W. P.). Diese Zellen ähneln weitgehend den Schreckstoffzellen der Ostariophysi (Pfeiffer, 1960). Karl von Frisch, Doktorvater des Zweit-Autors, forderte diesen bei seiner Abreise an die Zoologische Station in Neapel Anfang 1957 auf, den Mageninhalt von *C. acus* zu untersuchen. Dies geschah an 2 von Pierre Tardent zur

[1] In memoriam Prof. Dr. Pierre Tardent.

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Verfügung gestellten Exemplaren; beide enthielten Reste von Kleinkrebsen, wie an den schwarzen Komplexaugen deutlich zu erkennen war. Dieser Befund wurde Alfred Kaestner mitgeteilt und ist in dessen Lehrbuch nachzulesen (Kaestner, 1963, S. 1235). Zwanzig Exkursionen an das Laboratoire Arago in Banyuls-sur-mer (1963 und 1980 - 1999) ermöglichten *C. acus* zu beobachten, zu sammeln und mit ihm zu experimentieren. Im Mittelpunkt des Interesses standen dabei die Fragen nach seiner Häufigkeit und Verbreitung, seinem Habitat und der Bevorzugung verschiedener Seewalzen-Species, der Art und Weise seines Eindringens, der Verbleibdauer im Wirt und nicht zuletzt seiner Ernährung. Handelt es sich bei *C. acus* tatsächlich um einen Nahrungsparasiten, der Teile der Seewalze frißt, wie von Arnold (1953) behauptet aber nicht bewiesen und von der Sekundärliteratur kritiklos übernommen worden ist? Oder ist *C. acus* ein Inquilinist, dem die Seewalze lediglich als Wohnhöhle dient, wie von Emery (1880) beschrieben? Diesen Fragen sind wir im folgenden nachgegangen.

MATERIAL UND METHODEN

Alle Exemplare von *C. acus* wurden an der Küste vor Banyuls-sur-mer (Frankreich) gesammelt: 38 *C. acus* stammten aus 450 *Stichopus regalis* (Cuvier) (70 - 110 m Meerestiefe), nur 2 aus 85 *Holothuria tubulosa* Gmelin (weniger als 10 m Meerestiefe). Demgegenüber enthielten 142 *Holothuria polii* Delle Chiaje und 63 *H. tubulosa* aus der Bucht von Port de la Selva (weniger als 10 m Wassertiefe) keinen einzigen *C. acus*. Weil die Fische bisher fast ausschließlich in ihren Wirten und nahezu nie freischwimmend gefunden worden waren, konzentrierten wir uns beim Fang auf die als Wirte bekannten Aspidochirota *S. regalis*, *H. tubulosa* und *H. polii*. Die Seewalzen wurden mittels eines Schleppnetzes gesammelt, das in 70 - 110 m Tiefe 60 - 90 min lang parallel zur Tiefenlinie über den Grund gezogen wurde. Die dabei gefangenen *S. regalis* - die beiden anderen Species kommen in dieser Tiefe vor Banyuls-sur-mer nur äußerst selten vor - wurden an Bord in einem Behälter mit Meerwasserdurchlauf aufbewahrt und an Land aufgeschnitten, um zu prüfen ob sie *C. acus* enthielten. Beim Eröffnen ihrer physiologischen Unterseite mit einer kräftigen Präparierschere war es unerheblich, ob der Schnittansatz im Maul oder im After erfolgte. Die Fische können sich aufgrund ihrer flexiblen Wirbelsäule an dem der Einschnittstelle gegenüberliegenden Ende zu einem kleinen Knäuel zusammenrollen, so daß sie leicht zu übersehen sind (Abb. 2e). Wegen des grobmaschigen Schleppnetzes war nicht gewährleistet, daß freischwimmende *C. acus* oder solche, die von ihrer Seewalze mitsamt den Eingeweiden ausgestoßen worden waren, mitgefangen wurden. Um das Entkommen der Fische zu vermeiden, wurden *H. tubulosa* und *H. polii* von Hand gesammelt und unter Wasser in Plastiksäcken aufbewahrt. Beim Aufschneiden war erhöhte Vorsicht geboten, da die Arten von *Holothuria* eine wesentlich stärkere Hautmuskulatur besitzen als *S. regalis* und sich damit zu einer extrem harten Kugel zusammenziehen können. Alle *C. acus* wurden zusammen mit Seewalzen in Meerwasseraquarien gehalten. Die Versuche wurden in einem Glasaquarium (40 x 20 x 25 cm) und in einem Plastikaquarium (50 x 30 x 30 cm) durchgeführt. Um es den wegen der Fangbedingungen durch Dekompressionsschäden geschwächten Fischen zu ermöglichen in die Seewalze

zu gelangen, wurde der Wasserspiegel während der ersten Tage nach dem Fang bis auf Höhe des Afters der Seewalze gesenkt. Für die Beobachtung des Eindringens wurde jeweils ein *C. acus* zusammen mit einer *H. tubulosa* oder einem *S. regalis* in ein Aquarium gesetzt. Bei den Wahlversuchen bekam der Fisch immer eine *H. tubulosa* und einen *S. regalis*, die wahllos aus der Menge der vorhandenen Seewalzen herausgegriffen worden waren. Wenn *C. acus* in einer Seewalze verschwunden war, wurde das Verhalten des Wirtes mindestens 5 min weiter beobachtet, um zu prüfen ob der Fisch ihn wieder verläßt. Nach Versuchsende wurde *C. acus* mit der Seewalze wieder in das Hälterungsbecken zurückgesetzt. Die Dokumentation der Versuche erfolgte exemplarisch mittels Videokamera (Typ: Sony Video 8) und Photoapparat (Typ: Canon EOS 100). Ansonsten wurden schriftliche Protokolle erstellt. Um zu klären welche Faktoren für die Art des Einstiegs in die Seewalze verantwortlich sind, wurde das vor- und rückwärtige Eindringen der Fische in Einzelbildsequenzen aufgelöst. Zur Auswertung dieser Sequenzen dienten ein Videorecorder (Typ: Panasonic) und ein Computer (Programm: Scancam).

Auch alle für die anatomischen und histologischen Untersuchungen verwendeten *C. acus* Exemplare entstammten *S. regalis* aus 70 - 110 m Meerestiefe. Die Fische wurden in 10% Formalin oder nach Bouin fixiert und später in 70% Ethylalkohol überführt. Sie wurden anschließend vermessen, der Länge nach sortiert, numeriert und ihr Geschlecht anhand der Gonaden bestimmt. Im Labor wurden die Mägen von in Formalin fixierten *C. acus* unter dem Binokular geöffnet und auf ihren Inhalt untersucht. Die dabei gefundenen Kleinkrebse wurden mit Boraxkarmin gefärbt und in Kanadabalsam eingeschlossen. Bei nach Bouin fixierten Fischen wurden die Mägen ganz herauspräpariert und in Paraffin eingebettet. Von den Paraffinblöcken wurden 7µm dicke Schnitte angefertigt, mit Hämalaun-Eosin oder Azan gefärbt und unter einem Zeiss-Mikroskop ausgewertet und photographiert.

ERGEBNISSE

Die Häufigkeit von *C. acus* in *S. regalis* war in den verschiedenen Jahren sehr unterschiedlich: während 1995 im Juli 25 *C. acus* in 45 *S. regalis* gefunden wurden; waren es 1998 zur selben Jahreszeit nur 12 Fische in 329 *S. regalis*; 1996, 1997 und 1999 fischten wir keinen einzigen *C. acus*. Der Besatz von *S. regalis* mit *C. acus* war 1995 mit 55% viel höher als in allen anderen Jahren, obwohl alle Fänge zur gleichen Jahres- und Tageszeit im selben Gebiet stattfanden und auch die angewandten Fangmethoden, sowie Boot, Netz und Mannschaft immer die gleichen waren. Die beiden einzigen *C. acus* aus 85 *H. tubulosa* wurden 1998 in weniger als 10 m Meerestiefe über Felsgrund bei Banyuls-sur-mer gefunden.

Die *Stichopus*-Exemplare waren aus 70 - 110 m Tiefe geholt worden, weshalb alle enthaltenen Fische deutliche Dekompressionsschäden zeigten, die 3 - 4 Stunden nachdem sie auf Meereshöhe gebracht worden waren in Form von Gasbläschen auftraten. Im Bereich von Kopf und Magen bildeten sich Gasansammlungen, die manchmal zusätzlich über den ganzen Schwanz verteilt vorkamen. Weil der Auftrieb der Fische durch diese im Körper eingelagerten Gase erheblich erhöht wurde, war es ihnen

unmöglich im Aquarium zu den Seewalzen am Grund abzutauchen. Zudem wirkten die Fische extrem geschwächt. Nur in der Seewalze erholten sie sich; alle *C. acus*, die es nicht schafften sich in eine Seewalze zurückzuziehen, erlagen innerhalb weniger Tage ihren Verletzungen. Andere Exemplare mit ähnlich schwerwiegenden Dekompressionsschäden erholten sich in der Seewalze binnen maximal 3 Tagen und konnten danach auch bei normalem Wasserstand wieder zum After abtauchen um in die Seewalze einzudringen.

Wahlversuche: Da die meisten Individuen von *C. acus* in *S. regalis* gefunden worden waren, sollte überprüft werden ob *S. regalis* auch bei einer Wahlmöglichkeit bevorzugt wird. Alle Wahlversuche verliefen überraschend gleichförmig. *C. acus* zeigte immer ein ausgesprochenes Interesse an *H. tubulosa*, was am schnelleren und weiter ausholenden Schlängeln seines Schwanzes zu erkennen war. Stieß der Fisch zufällig zuerst auf *S. regalis*, machte er keinerlei Anstalten in sie einzudringen, sondern suchte das Aquarium weiter ab. Traf er zuerst auf *H. tubulosa*, ging er meist sofort in "Lauerstellung". Diese Stellung ist dadurch gekennzeichnet, daß Kopf und Rumpf regungslos bleiben während der Schwanz eine schnelle Schlängelbewegung durchführt. Der Körper nimmt dabei vor dem After der Seewalze eine horizontale Lage ein. Aus dieser Lauerstellung heraus versucht *C. acus* in den After der Seewalze zu gelangen sobald diese Atemwasser ausstößt. In insgesamt 11 Wahlversuchen mit 3 Fischen drangen alle ohne Ausnahme in *H. tubulosa* ein: Fisch Nr. 30 siebenmal, Nr. B und Nr. 31 je zweimal. In den Versuchen mit den Fischen Nr. B und Nr. 31 wurde jeweils einmal beobachtet, wie sie in eine schon besetzte *H. tubulosa* eindrangen, obwohl jedesmal ein unbewohnter *S. regalis* als Alternative zur Verfügung stand. Auch in anderen Versuchen hielten sich wiederholt 2 - 3 *C. acus* in einer *H. tubulosa* oder im selben *S. regalis* auf. Die Wahlversuche zeigten deutlich, daß *C. acus H. tubulosa* gegenüber *S. regalis* bevorzugt.

Einstiegsvarianten: *C. acus* kann auf 2 verschiedene Weisen in die Seewalze eindringen - Kopf oder Schwanz voraus. Kopf voraus Eindringen (Abb. 1): *C. acus* legt sich in Lauerstellung vor den After der Seewalze. Sobald sie ihren Atemwasserstrom durch den After ausstößt, beschleunigt der Fisch blitzschnell die Schlängelbewegungen seines Schwanzes und ist innerhalb von 40-80 ms vollständig in der Seewalze verschwunden. Dieser Vorgang ist manchmal so schnell, daß die Einzelbildanalyse keinen genauen Aufschlufl ermöglicht: bei *S. regalis*: oft schneller als 80 ms, manchmal aber auch 4, 10, 13, 50 und 65 s; bei *H. tubulosa* meist zu schnell um mit Aufnahmen von 25 Bildern/ s festgehalten werden zu können, oft 40-80 ms, nur ausnahmsweise mehrere Sekunden. Schwanz voraus Eindringen (Abb. 2a-c): Wenn *C. acus* rückwärts in die Seewalze einzudringen versucht, nimmt er zuerst dieselbe Lauerstellung ein wie beim Vorwärtseindringen. Jetzt ist aber zu beobachten, daß die Schwanzspitze sich immer wieder an der rechten oder linken Seite einzurollen und eine Schleife zu bilden beginnt. Spürt der Fisch den Wasserstrom der Seewalze, führt er den Schwanz an seiner Körperseite und am Kopf vorbei, den Körper gleichsam als Gleitschiene verwendend. Der Kopf dient dabei als Einfädelhilfe für den Schwanz, so daß dieser in den geöffneten Anus eingeführt werden kann. Die Fische bewegten hierbei den Schwanz in fast allen Fällen an ihrer linken Körperseite vorbei. Steckt der Fisch bereits mit der

ABB. 1. *Carapus acus* (Länge 115 mm): Vorwärtseindringen in *S. regalis*; a) Lauerstellung mit Maul am After der Seewalze; b) Kopf in Seewalze, kräftiger Schwanzschlag. (Fotos: T. Moritz)

Schwanzspitze im After der Seewalze, so biegt er seinen Körper nach einer Seite hoch, wodurch ihm anscheinend ein besserer Halt ermöglicht wird. Im Innern der Seewalze verkeilt er sich. Je nach Seewalzenart und Fischgröße dauerte es 12 - 472 s bis *C. acus* ganz in der Seewalze verschwunden war: bei *S. regalis*: 15, 34, 58, 102, 139 und 195 s; bei *H. tubulosa*: 12, 13, 32, 93, 110 und 472 s. Der Rückwärtseintritt währte mehr als doppelt so lang wie der Vorwärtseintritt. Unterbrechungen im Ablauf des Eindringens fanden an unterschiedlichen Stellen statt. Daß der Fisch dabei durch seine leicht abstehenden Brustflossen und Kiemendeckel behindert wird, war nicht zu erkennen. Nachdem *C. acus* ganz in der Seewalze verschwunden war, wurde wiederholt beobachtet wie er seinen Kopf durch den After der Seewalze teilweise herausstreckte und atmete (Abb. 2d). In manchen Fällen besaßen *S. regalis*-Exemplare, in welche Fische eindrangen, keine weiteren inneren Organe mehr außer Darmresten. Gonade und Wasserlunge waren bereits früher ausgeworfen worden. In diesen Fällen ist anzunehmen, daß der Fisch über dieselbe Öffnung der Enddarmerweiterung in die Leibeshöhle vordrang über die er in die Wasserlunge gelangen könnte. Problematisch wird die Erklärung allerdings für Fische, die in der Leibeshöhle von Seewalzen gefunden wurden, welche noch über ihre Wasserlunge verfügten. Es wird vermutet, daß sich der Fisch in der engen Wasserlunge umdreht und dabei das dünnhäutige Lungengewebe durchstößt.

Drei *S. regalis* wurden beobachtet wie sie auf das Eindringen des Fisches umgehend mit heftigem Schlängeln reagierten. Ihre Auf- und Abbewegungen dauerten bis zu 8 min und wurden auch durch Umsetzen in ein anderes Aquarium nicht unterbrochen; der *C. acus* im Innern verließ seine Behausung jedoch nicht. *H. tubulosa* versuchte durch Kontraktion ihres Afterschließmuskels und ihrer Hautmuskulatur im hinteren Körperabschnitt den Fisch am Eindringen zu hindern. Ihr Körper erschien dadurch im posterioren Bereich wesentlich dünner. Wie die lange Einstiegsdauer vermuten läßt, wurde dadurch das Vorhaben von *C. acus* zwar erschwert, doch nicht verhindert. In 2 Fällen kotete *H. tubulosa*, wodurch es ihr gelang den bereits teilweise eingedrungenen *C. acus* wieder herauszudrücken. Beide Male startete der Fisch sogleich einen weiteren Versuch, der jeweils schnell zum Erfolg führte. Häufigkeit und Verteilung der vor- und rückwärtigen Eintritte von *C. acus* hängen sowohl von der Größe des Fisches als auch von der Seewalzen-Species ab. Bei Fisch Nr. 30 (115 mm) halten sich die rück- und vorwärtigen Eintritte in *S. regalis* mit 9:7 etwa die Waage; bei *H. tubulosa* wurde dagegen der Rückwärtseinstieg mit 20:5 bevorzugt. Zwei weitere Fische entschieden sich mit 11:2 bzw. 7:0 ebenfalls für den Rückwärtseintritt. Der Wechsel zwischen den beiden Eintrittsvarianten erfolgte bei diesen Fischen mittlerer Körperlänge unregelmäßig. Größere Fische drangen dagegen immer mit dem Schwanz voran ein, egal ob sie *S. regalis* oder *H. tubulosa* vor sich hatten. Haut- und Schließmuskulatur sind bei *H. tubulosa* stärker entwickelt und kräftiger als bei *S. regalis*, bei dem sich der After auch in kontrahiertem Zustand leicht öffnen läßt. Der Fisch kann also auch mit seinem dicken Vorderende voraus eindringen. Anders ist die Situation bei *H. tubulosa*. Mit ihrer kräftigen Muskulatur verschließt sie den Anus so fest, daß es selbst mit einer dünnen Sonde nahezu unmöglich ist ihn zu öffnen. Hier steckt *C. acus*

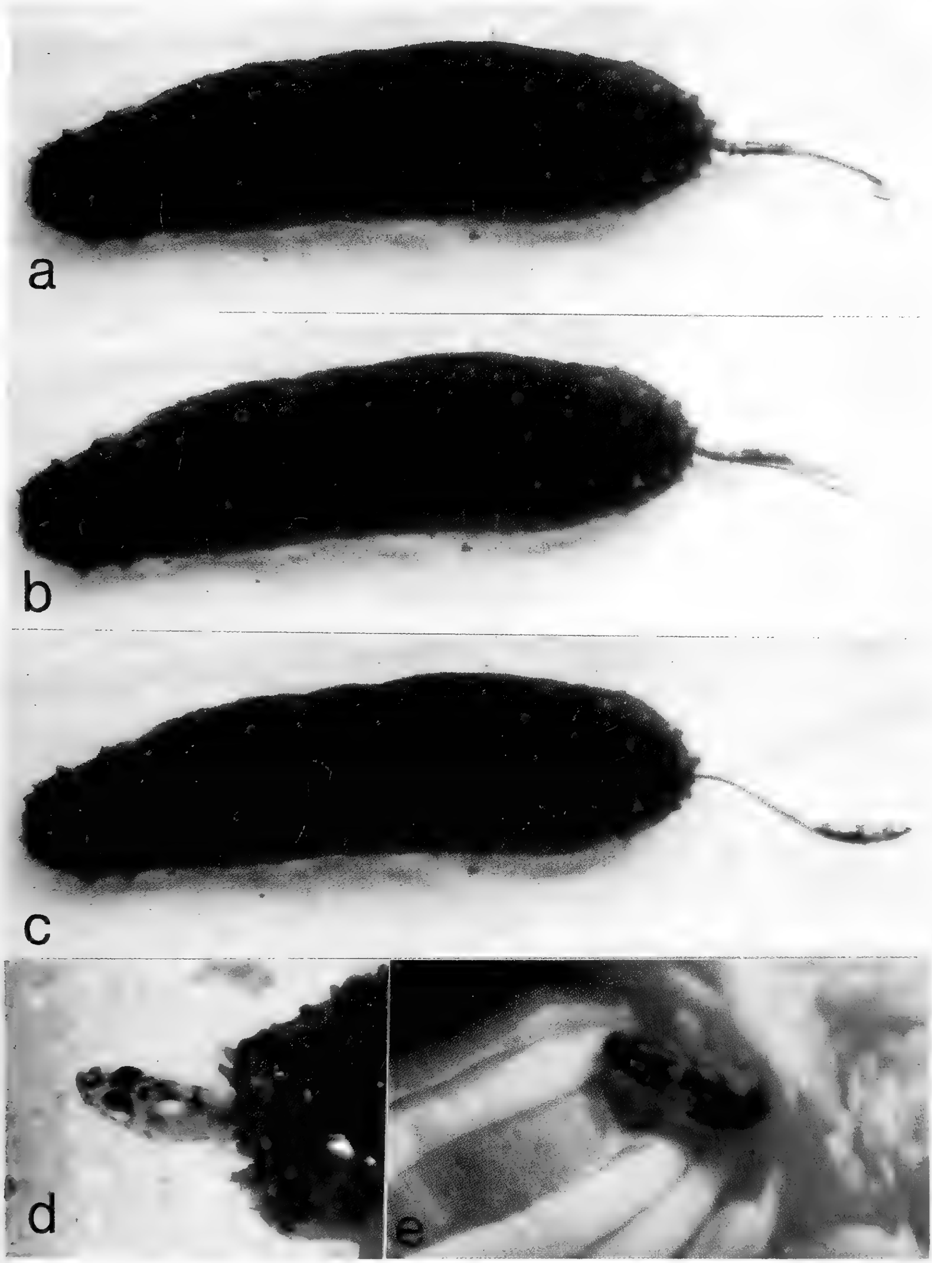

Abb. 2. *Carapus acus* (dasselbe Exemplar wie in Abb. 1): (a-c) Rückwärtseindringen in *H. tubulosa*; a) Einrollen der Schwanzspitze; b) Schwanz wird links am Körper vorbeigeführt; c) Fisch hat sich umgedreht, Schwanzspitze im After der Seewalze; d) Kopf von oben, in *S. regalis*; e) beim Freipräparieren in *S. regalis*. (Fotos: T. Moritz)

zuerst seinen spitz auslaufenden Schwanz als dünneres Körperende in den Anus. Ist der Schwanz erst einmal in der Seewalze, kann den Fisch fast nichts mehr davon abhalten ganz einzudringen. Handelt es sich bei dem Fisch um ein größeres Exemplar, verwendet er die Variante "Schwanz voraus" auch bei *S. regalis*, da sein Kopf für einen frontalen Vorstoß zu dick ist.

Mageninhalt: In histologischen Schnittpräparaten von 2 nach Bouin fixierten Mägen sind deutlich Komplexaugen von Kleinkrebsen zu erkennen. Dagegen konnten histologisch keine Hinweise darauf gefunden werden, daß *C. acus* auch Gewebe der Seewalzen fressen würde. Weder Gonaden noch Muskulatur oder sonstige zelluläre Strukturen von *S. regalis* befanden sich in den Fischmägen. In den Mägen von 2 in Formalin fixierten Fischen aus *S. regalis*, wurden 4 Kleinkrebse angetroffen bei denen es sich vermutlich um die Garnele *Pandalina* sp. (Decapoda) handelt (Fischer *et al.*, 1987). Insgesamt wurden in den Mägen von 4 der 17 untersuchten Männchen und Weibchen von *C. acus* (154 - 195 mm Gesamtlänge) Krebse oder deren Augen gefunden. Knapp 1/4 der Fische hatte also kurz vor seinem Fang Krebse gefressen.

DISKUSSION

VERBREITUNG: Die meisten Species der Gattung *Carapus* leben in tropischen oder subtropischen, überwiegend seichten Gewässern (Williams, 1984; Markle & Olney, 1990). *Carapus acus* ist auf das Mittelmeer und die angrenzende südliche Atlantikküste beschränkt. Arnold (1953, 1956) fand *C. acus* bei Neapel hauptsächlich in *H. tubulosa* aus 10 - 20 m Meerestiefe. Von 1350 bei Neapel in 10 - 25 m Tiefe gesammelten *H. tubulosa*-Exemplaren enthielten nur 19 (1,4%) einen *C. acus* (Gustato, 1976). Der Befall von nur 2 *H. tubulosa* bei Banyuls-sur-mer hatte den Anschein von Zufälligkeit, denn 38 von 40 *C. acus* fanden wir in *S. regalis* aus 70 - 110 m Tiefe. Die im Juli - August 1998 gefangenen *C. acus* waren überwiegend Jungfische (Gesamtlänge durchschnittlich 129 mm), von denen sich aber keiner mehr in einem Larvenstadium befand. Im Gegensatz dazu handelt es sich bei den 1995 zur selben Jahreszeit gefangenen Fischen hauptsächlich um große adulte Exemplare (Gesamtlänge durchschnittlich 173 mm), wobei der Befall 55% betrug. Im Meer haben wir zwar die meisten (38) *C. acus* in (450) *S. regalis* und nur 2 in (85) *H. tubulosa* gefunden, doch als wir die Fische im Labor vor die Wahl zwischen *S. regalis* und *H. tubulosa* stellten, entschied sich *C. acus* immer für *H. tubulosa*. Die Bevorzugung von *H. tubulosa* im Aquarium war überraschend, da deren Tiefenverbreitung im Untersuchungsgebiet von Banyuls-sur-mer großteils nicht mit der des Fisches übereinstimmt. Bei den zwei in geringer Tiefe in *H. tubulosa* gefangenen *C. acus* handelte es sich vermutlich um verirrte Individuen, obgleich *C. acus* in anderen Regionen vor allem in *H. tubulosa* aus geringer Tiefe gefischt wurde (Emery, 1880). Der Vergleich der Literaturangaben zur Tiefenverbreitung von *C. acus* zeigt hingegen, daß sich das Vorkommen des Fisches mit dem beider Seewalzen-Species in anderen Gebieten überschneidet (Abb. 3). Folgende Hypothese könnte die experimentelle Bevorzugung von *H. tubulosa* erklären. Geht man davon aus, daß sich der Fisch von Kleinkrebsen ernährt, wäre es gleichgültig welche Species er als "Wohnhöhle" aussucht. Wichtig wäre dagegen, welches Substrat die See-

walze bevorzugt, da auch die Beutekrebse untergrundspecifische Vorlieben haben. Die als Nahrung nachgewiesene *Pandalina* sp. lebt überwiegend auf Felsgrund. Auch *H. tubulosa* wurde meistens in Felsnähe gefunden. Als Substratfresser ist diese Seewalze zwar auf Sandgrund angewiesen, lebt jedoch vor Banyuls-sur-mer hauptsächlich an Orten, an denen die schützende Felsformation der Küste in sandigen Untergrund übergeht. Vor Banyuls-sur-mer ist dies in 5 - 20 m Tiefe der Fall. *S. regalis* kommt hingegen vorwiegend auf Sandgrund vor. So ließe sich erklären, warum *C. acus H. tubulosa* gegenüber *S. regalis* bevorzugt. In der nur bis ca. 25 m tiefen Bucht von Port de la Selva mit Sandgrund und *Posidonia*-Wiesen sind *H. tubulosa* und besonders *H. polii* zwar häufig, doch fehlen hier *C. acus* und *S. regalis*.

VERHALTEN: Aus einer Seewalze herauspräparierte und im Aquarium frei schwimmende *C. acus* zeigten zwei völlig unterschiedliche Schwimmweisen. Die einen schwammen an der Wasseroberfläche mit weit ausholenden schlängelnden Bewegungen und streckten dabei ihren Kopf immer wieder aus dem Wasser. Die anderen tauchten sofort Kopf voran zum Aquarienboden, wobei ihre schräge Schwimmlage beibehalten wurde bis sie auf eine Seewalze stießen. Arnold (1953) beschreibt ebenfalls diese beiden Schwimmweisen, deutet sie jedoch als Kennzeichen verschiedener Entwicklungsstadien. Nach Arnold (1953) schwimmen Tenuis-Larven mit weitausholenden Bewegungen während junge und adulte Fische nur leicht mit dem Schwanz schlängeln. Unsere Beobachtungen konnten diese Aussage nicht bestätigen. Vielmehr hatte es den Anschein, daß die Schwimmweise mit dem Allgemeinbefinden des Fisches zusammenhängt. Hatte er Dekompressionsschäden oder war der Sauerstoffgehalt im Aquarium zu niedrig, so schnappte er wiederholt an der Oberfläche nach Luft und schwamm mit hektischen Bewegungen. Das gleiche Verhalten zeigte er auch in Bedrängnis. Dagegen schwamm er bei gutem Allgemeinzustand in Schräglage mit dem Maul am Boden. Die beiden Schwimmweisen sind somit nicht abhängig vom Entwicklungsstadium sondern Ausdruck des Befindens. Wenn der Fisch vor dem After der Seewalze seine Lauerstellung einnimmt, sind die Bewegungen der Brustflossen deutlich zu erkennen. Diese Flossen schlagen abwechselnd und dienen sowohl der Balance als in geringem Maße auch der Lokomotion. Der Vortrieb erfolgt hauptsächlich über den Schwanz, wie beim Vorwärtseindringen zu sehen ist. Hierbei beschleunigt der Fisch in kürzester Zeit bis auf Höchstgeschwindigkeit durch kräftiges, weitausholendes Schwanzschlagen.

Carapus acus findet die Seewalzen vermutlich zufällig; ein besonderes Suchschema war nicht zu erkennen. Nach Arnold (1958) und Trott (1981) geschehe die Lokalisierung von weiter entfernten Zielen chemisch, während auf kurze Distanz die visuelle Orientierung eine Rolle spiele. Van Meter & Ache (1974) vermuten, daß nur die Lokalisierung des Afters über die Augen erfolgt. Unsere Fische schwammen im Aquarium umher bis sie auf eine Seewalze trafen. Ob und wie weit hierbei chemische, taktile oder visuelle Reize eine Rolle spielen, kann nicht entschieden werden. Die deutliche Reaktion auf das ausgestoßene Atemwasser ist wahrscheinlich taktil und chemisch bedingt. Eine visuelle Wahrnehmung ist nicht anzunehmen, da fast alle Versuchsfische aus 70 - 110 m Tiefe stammen und ihre Augen weitgehend rückgebildet sind. Die Beobachtung, daß vor allem kleinere Fische vorwärts in die Seewalze

eindringen, bestätigt Trott's (1981) Aussage, daß diese Weise die schnellste Möglichkeit des Eindringens darstellt. Die Entscheidung, ob ein Fisch vorwärts oder rückwärts eindringt, wird durch die morphologischen Gegebenheiten der Seewalzen-Species und die Fischgröße bestimmt, denn auch große Fische können vorwärts und kleine rückwärts eindringen. Zweimal wurden am Morgen Fische freischwimmend im Aquarium angetroffen, die sich am Vorabend noch in einer Seewalze befunden hatten. Ferner entwischten einige Exemplare in der Nacht durch die unzureichend gesicherten überläufe. Dies zeigt, daß *C. acus* die Seewalze nachts verläßt, vermutlich um auf Beutefang zu gehen. Einmal wurde beobachtet, wie ein *C. acus* seine *H. tubulosa* verließ nachdem er etwa eine halbe Stunde in ihr verweilt hatte. Der Fisch schwamm einige Runden im Aquarium und verschwand dann wieder in derselben Seewalze. Das selbständige Verlassen der Seewalze, ohne von ihr ausgeworfen zu werden, ist also möglich. Daß sich *C. acus* nicht dauernd in der Seewalze aufhält, zeigen auch die im Meer freischwimmenden Exemplare (Smith, 1964).

ERNÄHRUNG: Die anatomischen und histologischen Untersuchungen bewiesen, daß *C. acus* Krebse frißt. Fraglich blieb hierbei, ob diese sein ganzes Nahrungsspektrum ausmachen. Es gibt jedoch keinen Hinweis, daß *C. acus* seinen Wirt anfrißt. In keinem der untersuchten Mägen wurden Reste von *S. regalis* gefunden. Diese Befunde sprechen für die Annahme, daß *C. acus* kein Nahrungsparasit ist. Während der Verhaltensexperimente hatte *C. acus* nur Seewalzen zur Verfügung von denen er sich laut Arnold (1953) parasitisch ernährt. Eine andere potentielle Nahrung wurde in unseren Wahlexperimenten nicht angeboten. Auf separate Fütterungsversuche mit *Artemia* sp. oder lebenden Larven von *Mysis* sp. reagierte *C. acus* nicht. Wurden die Futtertiere ins Aquarium gebracht, so schwamm der Fisch sofort in die dunkelste Ecke ohne sich um die Krebse zu kümmern. *Pandalina* sp., die wir in den Mägen von *C. acus* gefunden hatten, war für uns als Futtertier nicht zugänglich. Gab man die Wasserlunge von *S. regalis* oder *H. tubulosa* ins Aquarium, war wiederholt zu beobachten, daß sich der Fisch neben oder unter der Lunge zusammenringelte. Kurzzeitig hatten wir deshalb die Coelomocyten der Seewalzen, die auch der Verdauung und Nährstoffspeicherung dienen, in Verdacht von *C. acus* aufgenommen zu werden. In diesem Fall müßten sich die Fische trinkend ernähren, indem sie die Coelomflüssigkeit der Seewalze schlucken um die in den Coelomocyten gespeicherten Stoffe zu verwerten. Zum einen besitzt *C. acus* keine Strukturen die einen filtrierenden Nahrungserwerb ermöglichen, zum anderen müflten gewaltige Mengen von Coelomocyten geschluckt werden um den Energiebedarf zu decken.

Um die Frage eines "Zubrotes" neben Futterkrebsen zu klären, wurde zum Vergleich die freilebende Carapinae-Art *Echiodon drummondi* Thompson, 1837 untersucht (Trott, 1981). Diese lebt in größeren Tiefen (bis ca. 300 m) vor den Küsten Britanniens, des südlichen Norwegens, des westlichen Dänemarks und in der Biskaya (Trott & Olney, 1986); sie ernährt sich von kleinen Invertebraten und Fischen. Achtzehn Exemplare von *E. drummondi*, die der Zweit-Autor 1985 vor Arcachon in der Biskaya in 200-300 m Meerestiefe gefangen und in Formalin fixiert hatte, wurden auf ihren Mageninhalt geprüft. In einem wurde ein vermutlich parasitischer Nematode gefunden, 6 andere enthielten Krebse. Wegen der fortgeschrittenen Verdauung waren 3

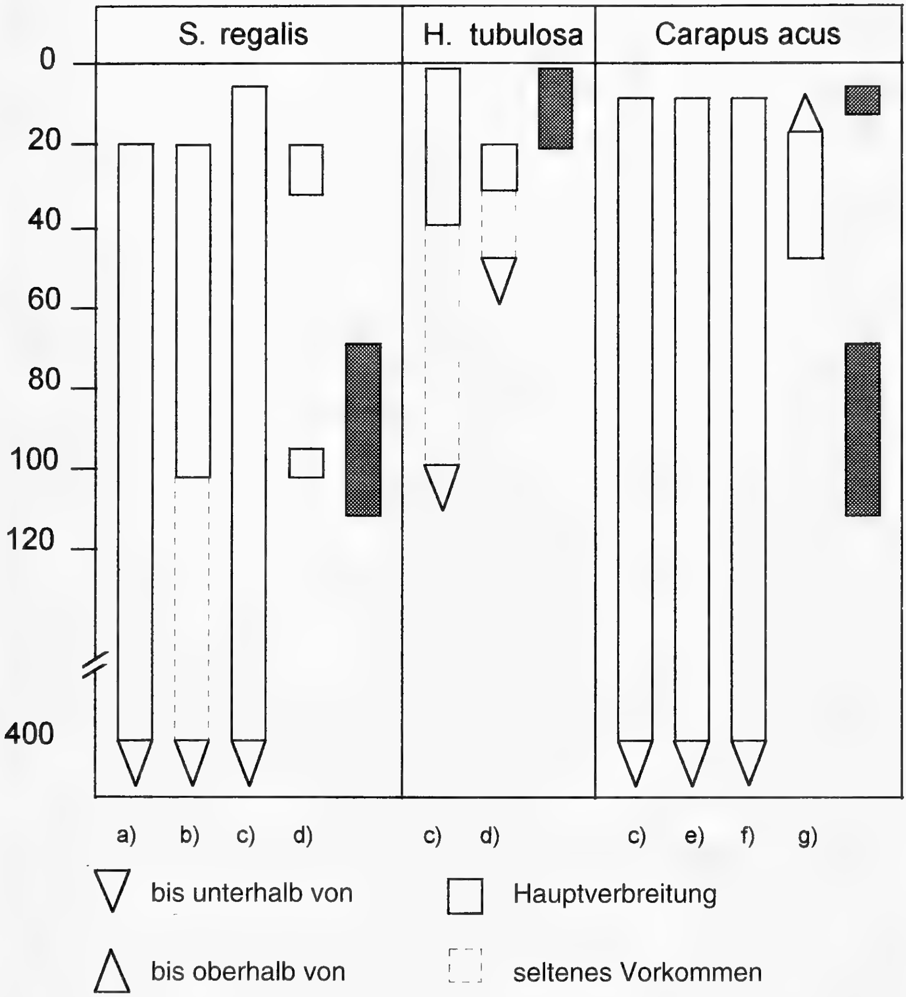

ABB. 3. Vertikale Verbreitung von *S. regalis*, *H. tubulosa* und *Carapus acus*: Vergleich der eigenen Befunde (schwarz) mit Literaturangaben (weiß) von: a) Nadal i Fortia (1981, 1994), b) Fiedler & Lieder (1994), c) Riedl (1983), d) Mayer (1937), e) Bauchot & Pras (1980), f) Fiedler (1991), g) Markle & Olney (1990). Ordinate: Tiefe in m.

Krebse nicht zu identifizieren, bei den 3 anderen handelte es sich um Isopoda. Insgesamt hatte also 1/3 der untersuchten Fische Crustaceen im Magen. Bei *C. acus* betrug der Anteil der Exemplare mit Krebsen im Magen etwa 1/4. Der Vergleich der beiden Werte legt die Vermutung nahe, daß auch *C. acus* kein Nahrungsparasit ist, sondern ein nachtaktiver Jäger. Es ist anzunehmen, daß die tagsüber gefischten *C. acus* ihr nächtliches Mahl bereits verdaut hatten. Demgegenüber müßten bei parasitischer

Ernährung, die keinem tageszeitlichen Faktor unterliegt, ständig Gonaden oder andere Gewebe von Seewalzen in den Fischmägen gefunden werden. Dies war in unserer Untersuchung jedoch nicht der Fall. Arnold (1953), der die parasitische Ernährung für *C. acus* postuliert, führt keinen Beweis für seine Spekulation an. Außerdem beobachtete Gustato (1976), daß von 17 *C. acus*, die er aus *H. tubulosa* entnahm, sich nur 2 in der Leibeshöhle befanden. Wie sollten die restlichen 15 Fische in der Wasserlunge von der Gonade fressen?

Um die Hypothese zu untermauern, wonach sich *C. acus* rein räuberisch ernährt, ist ein Vergleich mit den anderen Species der Gattung *Carapus* hilfreich. Für viele von ihnen wird ebenfalls eine räuberische Lebensweise angenommen. Krebse wurden gefunden im Magen von *C. bermudensis* (Smith *et al.*, 1981), *C. dubius* (Trott, 1970), *C. homei* (Smith, 1964) und *C. mourlani* (Trott, 1970). Auch *C. birpex* (Trott & Olney, 1986) und *C. parvipinnis* (Fiedler, 1991) werden nicht Parasiten genannt, sondern wie die vier vorher aufgelisteten Species als Kommensalen, Einmieter, Inquilinisten, Kannibalen oder Symbionten bezeichnet (Strasburg, 1961, Smith & Tyler, 1969; Seymour & Mc Cosker, 1970; Dawson, 1971, van Meter & Ache, 1974; Markle & Olney, 1980; Fiedler, 1981; Trott, 1981; Trott & Olney, 1986).

All diese Befunde stützen die Hypothese, wonach auch *C. acus* als Kommensale lebt. Als bessere ökologische Begriffe für die Lebensweise von *C. acus* können Endophoresie (Baer, 1951) und Entökie (Hohorst, 1981; Hentschel & Wagner, 1984) herangezogen werden. Am treffendsten erscheint uns die Bezeichnung Inquilinismus (Emery, 1880; Bertin & Arambourg, 1958; Trott, 1970; Trott & Olney, 1986), da sich der Fisch selbständig ernährt. Völlig fehl am Platz ist hingegen der Begriff Symbiose (van Meter & Ache, 1974; Gustato, 1976), da aus unserer Sicht die als Herberge dienende Seewalze keinerlei Vorteil von ihrem Mieter hat, der anscheinend allein profitiert. Aufgrund Arnold's (1953) unbewiesener Vermutung ist *C. acus* bisher zu Unrecht als Nahrungsparasit bezeichnet worden. Diese Behauptung wurde von der umfangreichen Sekundärliteratur übernommen (Bauchot & Pras, 1980; Riedl, 1983; Terofal, 1986; Fiedler, 1991; Fiedler & Lieder, 1994 u.a.), was zur heutigen allgemeinen Verbreitung dieser Ansicht führte. Es gibt jedoch bisher keinen einzigen Beweis dafür, daß *C. acus* von der Seewalze frißt und sich somit parasitisch ernährt. Die Seewalze dient ihm vielmehr nur als schützende Zuflucht zwischen seinen nächtlichen Beutezügen. *Carapus acus* muß dementsprechend als Inquilinist bezeichnet werden, wie dies Emery (1880) bereits völlig richtig getan hat - er nennt den Fisch "inquilino"!

SUMMARY

450 *Stichopus regalis* (Cuvier), caught with a trawl-net at a depth of 70 - 110 m off Banyuls-sur-mer (France), contained 38 pearlfish, *Carapus acus* (Brünnich). Two pearlfish were found in 85 *Holothuria tubulosa* Gmelin caught at Banyuls-sur-mer in less than 10 m of seawater. In contrast, 63 *H. tubulosa* and 142 *H. polii* Della Chiaje, collected by diving in the bay of Port de la Selva (ca. 10 miles south of Banyuls), did not contain any *C. acus*. Pearlfish collected from 1995 to 1998 were preserved to study

their stomach contents. Twelve individuals sampled in the summer of 1998 were kept in aquaria to analyse their behaviour by means of computer analysis of video records. Due to severe damage caused by insufficient decompression only a few individuals survived longer than one week after being placed in an aquarium. Since most *C. acus* were collected from *S. regalis*, the host preference of the fish was tested in an aquarium. *S. regalis* and *H. tubulosa* were provided as potential hosts. The results were surprising: in 11 experiments the 3 fish examined entered only *H. tubulosa* if they could choose between both species.

The entry of the pearlfish through the anus of the host holothurian may be head first or tail first. The pearlfish, in a head-down position, lies in wait in front of a sea cucumber. As the sea cucumber discharges its respiratory water the fish rapidly flicks its tail and enters the host. In the case of *H. tubulosa* the pearlfish enters head first within 40 - 80 ms; in *S. regalis* it takes up to 4 - 60 s. Tail first entry of *C. acus* takes 12 - 120 s. To enter the host, the pearlfish bends up its tail towards the head and its whole body forms a loop. When the waiting pearlfish perceives the water discharged by a holothurian, it moves its tail foreward along the side of its body and head. By this, the head helps the tip of the tail to target the anus of the host. Three *S. regalis* responded to intruding pearlfish with intense up and down movements; *H. tubulosa* contracted the sphincter of its anus and the spherical muscles of its body wall in the posterior region, whereby they became thin. However, neither defence method prevented *C. acus* from entering its host. In *C. acus* the frequency of head first and tail first entries depended on the size of the pearlfish and on the species of the host holothurian. A 145 mm long pearlfish entered *S. regalis* 9 times tail first and 7 times head first. However, the same fish entered *H. tubulosa* 20 times tail first and only 5 times head first.

The presence of *C. acus* in *S. regalis* sampled was extremely variable. In 1995 as many as 25 *C. acus* were collected from 45 *S. regalis* specimens. However, since 1996 only 13 *C. acus* were found in 405 *S. regalis*, although the locality, depth, season, day time, boat, trawl-net, sampling method and techniques, and even the crew were the same. The *C. acus* specimens sampled in 1995 were large (Ø 173 mm) and adult, whereas the pearlfish caught in 1998 were much smaller (Ø 129 mm) and mostly juvenile.

Pearlfish removed from the host holothurian demonstrated two completely different styles of swimming. Either they swam at the water surface with wriggling movements, repeatedly raising their head out of the water, or they immediately dived to the ground of the tank, maintaining a 30 - 40 degree tilted head-down position until they found a host holothurian. The latter style of swimming is only exhibited by healthy individuals. Swimming at the surface indicates either damage caused by insufficient decompression or a poor physical condition of the pearlfish.

In the aquarium it was found that pearlfish occasionally leave their host holothurians, especially at night, when they presumably feed. The stomachs of 4 out of 17 individuals contained small shrimps, probably *Pandalina* sp. In comparison, isopods and other small crustaceans were found in the stomachs of 6 out of 18 specimens of the closely related, but free-living, *Echiodon drummondi* Thompson. The statement by Arnold (1953) that *C. acus* is a parasite which feeds on the organs (gonads etc.) of its

sea cucumber host could not be confirmed. This statement is completely speculative and not based on any research results. The stomachs of *C. acus* examined did not contain any holothurian tissue. All other species of the genus *Carapus* feed on small invertebrates and fish, and none feed parasitic. Our results give reason to agree with Emery (1880), who stated that *C. acus* is an inquiline ("inquilino"), to whom the host holothurian serves as a shelter only.

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Un nouveau Collembole Neanurinae du Sud du Vietnam, *Blasconura batai* sp. n., avec une clé des espèces du genre (Collembola: Neanuridae)

Anne BEDOS & Louis DEHARVENG
Laboratoire d'Ecologie Terrestre, UMR 5552 du CNRS,
U.P.S., 118 route de Narbonne, 31062 Toulouse Cedex 4, France.
E-mail: deharven@cict.fr

A new neanurine springtail from southern Vietnam, *Blasconura batai* sp. n., with a key to the species of the genus (Collembola: Neanuridae). - The new species is described from a karstic area in southern Vietnam. A checklist and a key of all species of the genus *Blasconura* are given.

Key-words: Collembola - Neanuridae - Vietnam.

INTRODUCTION

Les collines de Hon Chong, isolées en bordure du Golfe de Thaïlande dans le Sud du Vietnam, constituent un remarquable site karstique dont une grande partie a été récemment détruite par l'extension de carrières pour l'exploitation du calcaire. Nous avons pu y réaliser quelques récoltes qui nous ont permis de décrire deux espèces de Collemboles, *Lepidonella lecongkieti* Deharveng & Bedos, 1995 et *Rambutsinella honchongensis* Deharveng & Bedos, 1996. Nous décrivons dans le présent travail une troisième espèce de cette région, *Blasconura batai* sp. n., et proposons une clé des espèces du genre *Blasconura.*

Blasconura Cassagnau, 1983

Le genre *Blasconura* a été créé pour l'espèce *Achorutes hirtellus* Boerner, 1906 de Java. La description originale de cette espèce, très sommaire, peut s'appliquer à de nombreux Neanurinae tropicaux de la tribu des Paleonurini. Il n'est donc pas étonnant, étant donné la confusion systématique qui régnait au sein des Neanurinae avant les mises au point de Cassagnau (1983, 1986, 1989), que l'espèce *hirtella* ait été signalée dans de nombreuses régions d'Asie du Sud-Est jusqu'en Australasie. Cette vaste distribution concerne probablement des espèces différentes, comme en témoignent les illustrations données dans la littérature (Handschin, 1926; Womersley, 1933, 1936; Denis,

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1948; Yosii, 1959, 1966; Gapud, 1968). Aucune de ces formes ne peut être attribuée sans ambiguïté au véritable *B. hirtella* tel que l'a redécrit Yosii (1976) d'après un matériel topotypique de Bogor (Java), ce que confirment nos propres observations sur de nouveaux exemplaires provenant de la localité-type. Autrement dit, toutes les citations de *B. hirtella* antérieures au travail de Yosii (1976) devront être révisées.

En 1988, Cassagnau décrit 6 *Blasconura* nouveaux d'Inde et de Sri Lanka; il suggère alors de placer *Achorutes separatus* Denis, 1934 du Vietnam dans le genre *Blasconura*. En suivant cette conception, ce sont 9 espèces qui peuvent être rapportées à ce genre:

- *Blasconura hirtella* (Boerner, 1906) sensu Yosii (1976)
  = *Achorutes hirtellus* Boerner, 1906
  = *Vitronura hirtella*; Yosii (1976), Yoshii (1981), Yoshii & Suhardjono (1989)
  = *Blasconura hirtella*; Cassagnau (1983, 1988)
  = *Vitronura* (*Blasconura*) *hirtella*; Yoshii & Suhardjono (1992)

espèce décrite de Java et citée d'autres îles indonésiennes (Halmahera et Kei, Yoshii & Suhardjono, 1992), de Thaïlande et de Singapour (Yosii, 1976), et de Malaisie (Sabah, Yoshii, 1981). Les citations du Vietnam et des Philippines reprises par Yoshii & Suhardjono (1989) d'après d'anciennes descriptions de Denis (1948) et Gapud (1968) sont à vérifier (cf. ante). La citation de Taiwan (Yoshii, 1981) demande également confirmation.

- *B. separata* (Denis, 1934) comb. n. (Vietnam)
  = *Achorutes separatus* Denis, 1934
- *B. anamalensis* Cassagnau, 1988 (Inde)
- *B. ceylonica* Cassagnau, 1988 (Sri Lanka)
- *B. palniensis* Cassagnau, 1988 (Inde)
- *B. prabhooi* Cassagnau, 1988 (Inde)
- *B. sholica* Cassagnau, 1988 (Inde)
- *B. toda* Cassagnau, 1988 (Inde)
- *B. batai* sp. n. (Vietnam).

Clé des espèces du genre *Blasconura*

1	Tubercules antennaires soudés entre eux et soudés au frontal en une seule masse	2
-	Tubercules antennaires soudés entre eux mais séparés du frontal; griffe sans dent	7
2	Soie O absente sur le tubercule antenno-frontal; griffe avec une dent	3
-	Soie O présente sur le tubercule antenno-frontal	5
3	Ant. I avec 7 soies; macrochètes écailleux; formule des Di: 122/22222	*batai* sp. n.
-	Ant. I avec 9 soies	4
4	Macrochètes plumeux; formule des Di: 133/22223	*hirtella*
-	Macrochètes longs et lisses; formule des Di: 244/33333	*toda*

5 Griffe sans dent; ant. I avec 8 soies; macrochètes raides, légèrement rugueux; formule des Di: 133/22222-3 . . . . *ceylonica*
- Griffe avec une forte dent; ant. I avec 7 soies; formule des Di: 134/44433 6
6 Macrochètes longs, fortement barbelés dans le tiers distal . . . . *sholica*
- Macrochètes courts, faiblement écailleux . . . . *prabhooi*
7 Soie O absente sur la tête; ant. I avec 7 soies; macrochètes faiblement rugueux; formule des Di: 122/22223 . . . . *anamalensis*
- Soie O présente 8
8 Soie O sur les tubercules antennaires soudés; un tubercule supplémentaire entre Di et De sur th. II à abd. III; macrochètes fortement barbelés et renflés à l'apex; formule des Di: 233/33333; ant. I avec 9 soies . . . . . *palniensis*
- Soie O sur le tubercule frontal; pas de tubercule supplémentaire sur th. II à abd. III; macrochètes ciliés; formule des Di: 333/22222; nombre de soies sur ant. I inconnu . . . . *separata*

Blasconura batai sp. n.

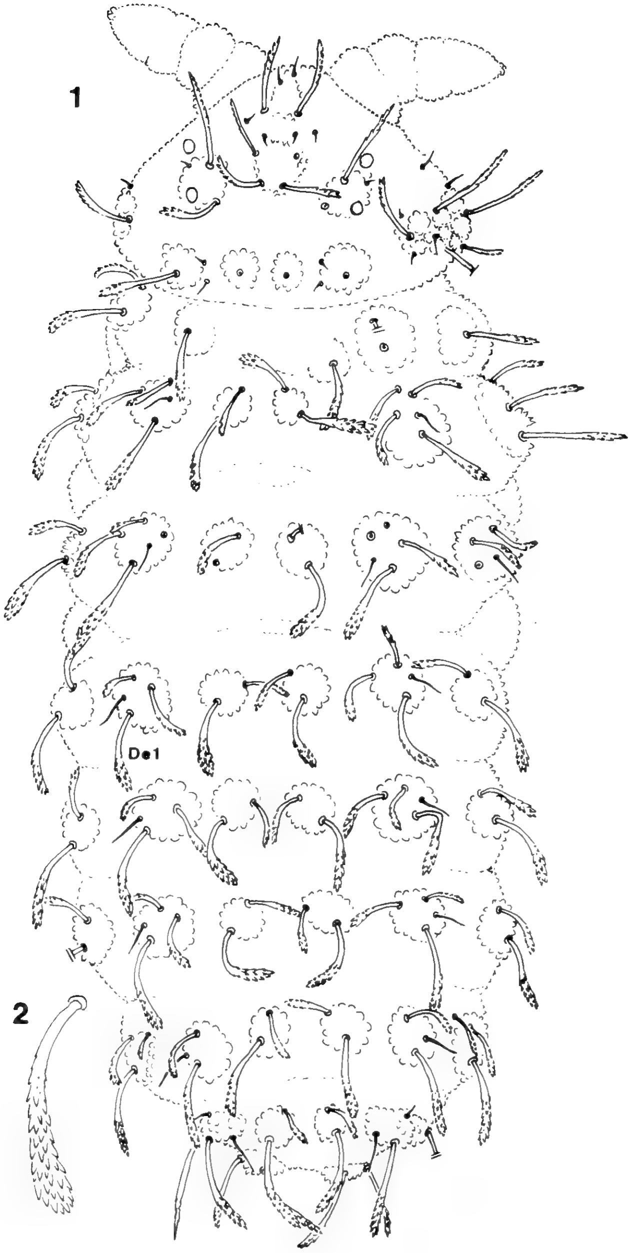
MATÉRIEL TYPE. Holotype femelle et 4 paratypes (2 femelles, 1 mâle subadulte et 1 juvénile) en préparation microscopique, 1 paratype juvénile en alcool. Vietnam: province de Kien Giang, Hon Chong, colline calcaire de Ba Tai, Berlese de litière dans un maquis, 19/12/1994 (relevé VIET-034). Holotype et 3 paratypes déposés au Laboratoire d'Ecologie Terrestre (Université Paul Sabatier, Toulouse, France), 2 paratypes déposés au Muséum d'histoire naturelle de Genève (Suisse).

Les abréviations utilisées dans la description sont celles définies par Deharveng (1983) et Deharveng & Weiner (1984). Le matériel étudié a été récolté par les auteurs.

DESCRIPTION: Longueur: 0,84 à 1,13 mm. Couleur: rouge sur le vivant, blanche en alcool, yeux non pigmentés. Habitus assez trapu et convexe (fig. 1). Tubercules dorsaux bien délimités mais peu convexes; grain tertiaire marqué par des groupes de grains secondaires non soulignés par de véritables réticulations. Abd. VI bilobé, visible dorsalement. Soies ordinaires dorsales de 2 types: quelques soies fines, lisses et pointues (mésochètes ou microchètes); macrochètes plus ou moins longs, courbes, élargis dans leur partie distale en forme de massue, avec une ciliature courte, serrée et imbriquée, en forme de pousse d'asperge (fig. 2). Soies S fines, atteignant 1/3 (sur le thorax) à 1/2 (à l'arrière de l'abdomen) de la longueur du macrochète voisin.

Tête (fig. 1, tab Ia et b). Soies S d'ant. IV de taille moyenne, subégales, relativement fines; vésicule apicale nettement trilobée. Ant. I avec 7 soies. Cône buccal fort; labre ogival assez large, avec 2/2,2 soies (les soies distales longues, dépassant l'apex du labre). Maxille styliforme, mandibule fine à 3 dents. 2+2 cornéules non pigmentées, la cornéule antérieure est extérieure et en avant du tubercule oculaire. Tubercules An et Fr fusionnés, séparés de Oc et de CL. Tubercules Di et De faiblement différenciés, non fusionnés. Tubercules DL, L et So soudés. Soies O et E absentes. Microchètes Di2 et De2 sur la bordure interne du tubercule De.

Thorax et abdomen. Tuberculisation et chétotaxie illustrées sur la figure 1 et le tableau Ic. Sur abd. IV, le macrochète Di2 est deux fois plus court que le macrochète Di1. Dent interne présente sur la griffe. Soie M absente sur le tibiotarse.



FIGS 1-2. *Blasconura batai* sp. n. 1: habitus et chétotaxie dorsale (longueur du corps: 0,94 mm); une soie surnuméraire est présente sur le tubercule De de th. II (côté droit); 2: macrochète De1 d'abd. I (longueur de la soie: 73 µm).

REMARQUE: L'holotype présente une anomalie sur th. II (fig. 1). Les 4 paratypes examinés sont également asymétriques pour la chétotaxie d'au moins un de leurs tergites. Une forte proportion d'exemplaires non symétriques n'est pas rare chez certains Neanurinae de la tribu des Lobellini, mais reste exceptionnelle chez les Paleonurini.

DERIVATIO NOMINIS: Le nom de l'espèce est celui de la localité-type, la colline de Ba Tai, une des rares collines du karst de Hon Chong qui devrait être épargnée par les carrières de calcaire.

TABLEAU Ia - Chétotaxie céphalique dorsale de *Blasconura batai* sp. n.

	Tubercule	Nombre de soies	Type de soies	Soies
CL	+	4	ML	F
			mé	G
Af	+	8	ML	A,B
			mi ou mé	C,D
Oc	+	3	ML	Ocm, Ocp
			mi	Oca
Di	+	1	ML	Di1
De	+	3	ML	De1
			mi	Di2, De2
DL+L+So	+	15	ML	4 soies
			Mc	1 soie
			mé	7 soies
			mi	3 soies

TABLEAU Ib - Chétotaxie céphalique ventrale de *B. batai* sp. n.

Vi	6
Ve	5-6
Labrum	2/2,2
Labium	10,0x?
Ant. I-II	7,11
Ant. III	17+5S
Ant. IV	or+8S+i+?mou

TABLEAU Ic - Chétotaxie postcéphalique de *B. batai* sp. n.

	Di	De	DL	L	Scx2	Cx	Tr	Fé	Ti
Th. I	1	2	1	-	0	3	6	?	18
Th. II	2	3+S	3+S+ms	3	2	7	?	?	18
Th. III	2	4+S	3+S	3	2	8	?	11	17
Abd. I	2	3+S	2	3	TV=4+4				
Abd. II	2	3+S	2	3	Ve=3-4 (Ve1 absent)				
Abd. III	2	3+S	2	4	Fu=4,0mi			Ve=3-4	
Abd. IV	2	2+S	3	6	Ve=7			VL=5	
Abd. V	2	——3+S——		(3)-4	Ag=3-(4)+3-(4)			VL avec L	
Abd. VI	——————7——————				Ve=14			An=2-3	

DISCUSSION

Deux espèces de *Blasconura* étaient déjà connues du Vietnam:

- *Blasconura* sp., signalée sous le nom de *Achorutes hirtellus* Boerner, 1906 du "Centre Annam", à Bana près de Tourane (Denis, 1934, 1948); il s'agit probablement d'une espèce inédite qui diffère du vrai *B. hirtella* de Java notamment par la présence de 3+S soies De (au lieu de 2+S) sur abd. IV.
- *B. separata* (Denis, 1934), signalée sous le nom de *Achorutes separatus* Denis, 1934 du "Tonkin", province de Phu-Ho, près de Yenbai (Denis, 1934, 1948).

Blasconura batai sp. n. est proche de la première de ces espèces mais possède une chétotaxie dorsale nettement plus réduite. La nouvelle espèce partage avec *B. hirtella* et *B. toda* les caractères suivants: la soudure des tubercules An et Fr, l'absence de soie O sur la tête et la présence d'une dent à la griffe; *B. batai* sp. n. se distingue de ces deux espèces par plusieurs caractères chétotaxiques, en particulier la présence de 7 soies sur ant. I au lieu de 9.

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Die Leucospidae (Hymenoptera: Chalcidoidea) der Schweiz, mit einem Bestimmungsschlüssel und Daten zu den europäischen Arten

Hannes BAUR[1] & Felix AMIET[2]
[1] Abteilung Wirbellose Tiere, Naturhistorisches Museum, Bernastrasse 15, CH-3005 Bern, Schweiz.
E-mail: hannes.baur@nmbe.unibe.ch
[2] Forststrasse 7, CH-4500 Solothurn, Schweiz.

The Leucospidae (Hymenoptera: Chalcidoidea) of Switzerland, with a key and data on the European species. - In this paper the taxonomy and distribution of the Swiss species of *Leucospis* Fabricius are presented. Four of the seven European species are recorded for Switzerland: *L. biguetina* Jurine, *L. dorsigera* Fabricius, *L. gigas* Fabricius, and *L. intermedia* Illiger. Except for *L. dorsigera* the main distribution lies in the Southern parts of the country. The altitudinal gradient ranges from the colline to the subalpine belt. Adults appear from May to September. *L. biguetina* and *L. gigas* are considered vulnerable with regard to the Swiss fauna. Almost exclusively females of *L. biguetina* and *L. gigas* are known from the study area, hence these species are likely to reproduce by thelytoky. A key, diagnoses, morphometric and distributional data are also given for the other two European species, *L. bifasciata* Klug and *L. brevicauda* Fabricius. The hosts of all species are critically reviewed and new hosts are recorded for *L. dorsigera* and *L . gigas*.

Key-words: *Leucospis* - taxonomy - key - distribution - new host records - Switzerland - Europe.

EINLEITUNG

Die Leucospidae stellen mit einer Grösse von ca. 4-16 mm die auffallendsten Vertreter der zumeist winzigen Erzwespen (Chalcidoidea) dar. Die Familie ist weltweit mit ca. 140 Arten in 4 Gattungen verbreitet (Bouček, 1974; Noyes, 1998), wobei in Europa nur gerade 7 Arten der Gattung *Leucospis* Fabricius vorkommen. Durch die verdickten Hinterbeine, den über den Gaster nach vorne gebogenen Legebohrer und die gelb-schwarze Zeichnung sind sie unverkennbar. Alle europäischen Arten führen eine parasitische Lebensweise, d. h. die Larven entwickeln sich als Ectoparasitoide an Larvenstadien von Wildbienen, z. B. *Anthidium*, *Megachile* oder *Osmia* (Apidae: Megachilinae) (Clausen, 1940; Bouček, 1974).

Erste Hinweise auf die Leucospiden der Schweiz finden sich bereits in Sulzer's Geschichte der Insekten (1776), wo unter der treffenden Bezeichnung 'Schenkelwespe' nicht wie angegeben *L. dorsigera* sondern *L. gigas* aufgrund von Exemplaren

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TABELLE 1

Morphologische Terminologie, sortiert nach Abkürzung bzw. Begriff (vgl. Abb. 1a-1d, gegenüberliegende Seite).

Ag	Auge	Auge	Ag
Cly	Clypeus	Clypeus	Cly
Co1	Procoxa	Dorsellum	Do
Co2	Mesocoxa	Gastraltergum	Gt
Co3	Metacoxa	Mesepisternum	Mep
Do	Dorsellum	Mesocoxa	Co2
Fe1	Profemur	Mesofemur	Fe2
Fe2	Mesofemur	Mesoscutum	Msc
Fe3	Metafemur	Mesotarsus	Ta2
Gt	Gastraltergum	Mesotibia	Ti2
Mep	Mesepisternum	Metacoxa	Co3
Mpl	Metapleuron	Metafemur	Fe3
Msc	Mesoscutum	Metapleuron	Mp1
Pe	Pedicel	Metatarsus	Ta3
Ppd	Propodeum	Metatibia	Ti3
Prn	Pronotum	Pedicel	Pe
Sca	Scapus	Procoxa	Co1
Scr	Scroben	Profemur	Fe1
Sct	Scutellum	Pronotum	Prn
Ta1	Protarsus	Propodeum	Ppd
Ta2	Mesotarsus	Protarsus	Ta1
Ta3	Metatarsus	Protibia	Ti1
Ti1	Protibia	Scapus	Sca
Ti2	Mesotibia	Scroben	Scr
Ti3	Metatibia	Scutellum	Sct

aus Genf beschrieben und illustriert wird. Fuessly (1783) meldet in seinem Beitrag zur Lebensweise von '*L. dorsigera*' ebenfalls Funde von *L. gigas* aus Genf und der Gegend von Zürich. Etwas später beschreibt Jurine (1807) in seinen «Nouvelle méthode de classer les hyménoptères et les diptères» neu *L. biguetina* Jurine aus der Schweiz (vgl. Bouček, 1974), daneben erwähnt er auch die Arten *L. dorsigera* und *L. gigas*. Hagenbach (1822) stellt aus der Umgebung von Basel *L. fuesslini* Hagenbach auf, ein Synonym von *L. dorsigera* (vgl. Bouček, 1974). Labram & Imhoff (1836) beschreiben und illustrieren letztere und fügen an, dass in der Schweiz noch 2-3 weitere Arten vorkämen. Von Chevrier (1870) erhalten wir unter *L. lepida* Chevrier eine weitere Fundortsangabe von *L. dorsigera* (vgl. Bouček, 1974) aus dem Genferseegebiet. Schliesslich zählt Schletterer (1890) in seiner bedeutenden, weltweiten Revision der Leucospiden eine Reihe neuer Funde für die erwähnten Arten in der Schweiz auf und führt zusätzlich *L. intermedia* für das Wallis an. Spätere Arbeiten (z. B. Bouček, 1959, 1974; Madl, 1990; Schmiedeknecht, 1930) enthalten kaum neue Angaben und zitieren zumeist in allgemeiner Form aus älteren Schriften.

Während wir recht gut über die Fauna vieler europäischer Ländern unterrichtet sind (Bouček, 1959, 1964, 1970, 1977; Berland, 1934b; Madl, 1989, 1990; Pagliano, 1998; Schletterer, 1890; Schmid-Egger, 1995), fehlte es bislang an einer übersichtlichen Darstellung der Leucospiden der Schweiz. Zudem förderte allein die grobe Durchsicht der Sammlungen von wenigen Museen ein reiches, unpubliziertes

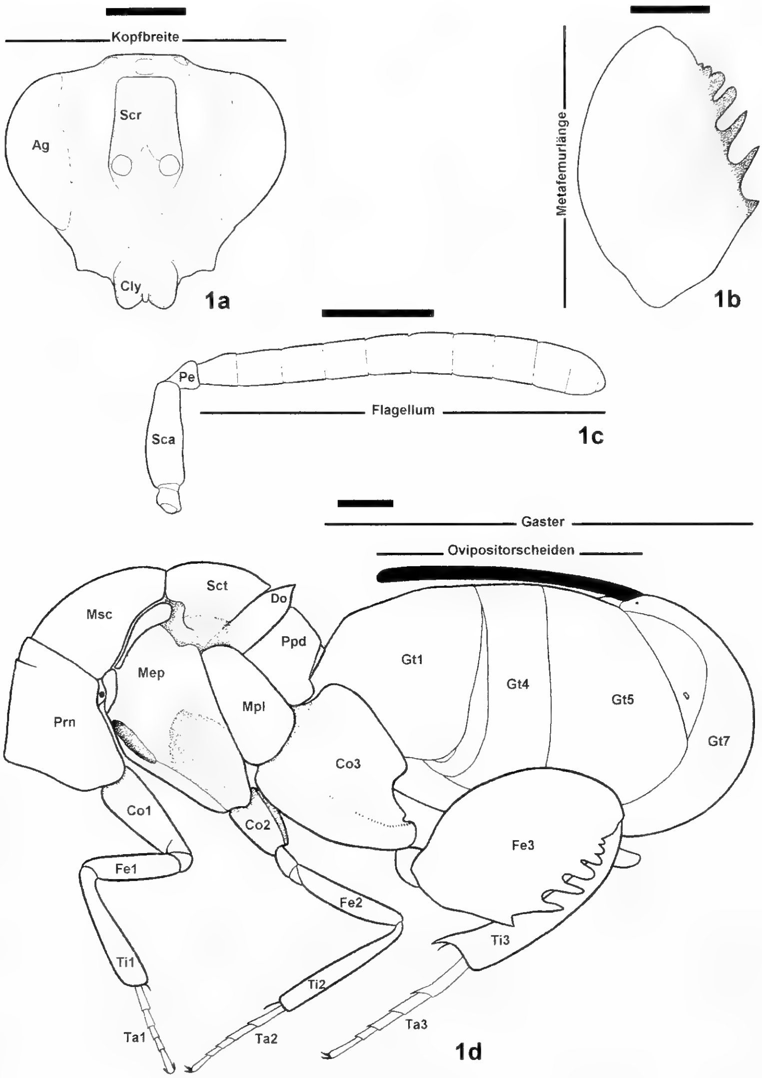


ABB. 1a-d, *L. gigas* ♀: Kopf frontal (a), Metafemur lateral (b), Antenne lateral (c), Körper ohne Kopf lateral (d) (vgl. Tab. 1, gegenüberliegende Seite). Massstab 1 mm.

Material aus dem Gebiet zutage. Mit der vorliegenden Arbeit wird erstmals die Verbreitung der Arten in der Schweiz umfassend dargestellt. Hierzu wurde das Material von sämtlichen grösseren Sammlungen der Schweiz und mehreren Museen im Ausland systematisch aufgearbeitet. Die Daten wurden im Hinblick auf eine Gefährdung der Arten in der Schweiz ausgewertet. Aufgrund von Funddaten der Wirte wurde versucht, den Grad der Übereinstimmung in der Verbreitung von Wirt und Parasitoid in der Schweiz aufzuzeigen. Ferner wurde für alle europäischen Arten die Literatur nach Wirtsangaben durchgesehen, welche kritisch analysiert und durch

neue Daten ergänzt wurden. Schliesslich werden ein Bestimmungsschlüssel, Diagnosen und morphometrische Daten zu allen europäischen Arten vorgelegt.

MATERIAL UND METHODEN

Die vorliegende Studie wertet Daten von insgesamt 919 Exemplaren aus der Schweiz (572) und Teilen von Europa, dem Nahen Osten und Nordafrika (347) aus. Für die Verbreitungskarten und die Diagramme zur Höhenverbreitung sowie Phänologie wurde ausschliesslich Material aus der Schweiz verwendet. Den Diagnosen und Messungen liegt das bei den einzelnen Arten aufgelistete Material zu Grunde. Die betreffenden Exemplare wurden mit einer Etikette mit dem Vermerk «Baur» und einer Seriennummer versehen. Messungen wurden an getrocknetem Material unter einem Stereomikroskop (Leica MZ12) bei 6 (Körperlänge) bzw. 20facher (alle übrigen Masse) Vergrösserung mit Hilfe eines geeichten Okular-Mikrometers (12 mm unterteilt in 120 Einheiten) durchgeführt, anschliessend wurden die Werte in Millimeter umgerechnet. Die Körperlänge entspricht der Länge vom Vertex bis zur Spitze des Gasters. Diese Messungen können systematische Effekte (Fehler) aufweisen, welche von den unterschiedlichen Konservierungsmethoden der einzelnen Sammler (z. B. die Streckung bzw. Krümmung von Individuen in einer bestimmten Weise) herrühren. Die Kopfbreite, die Metafemur- und die Ovipositorscheidelänge sind frei von systematischen Effekten. Die betreffenden Messstrecken sind aus den Abbildungen 1a, 1b und 1d ersichtlich. Der Beginn der Ovipositorscheide (vgl. Abb. 1d) ist gekennzeichnet durch eine feine Kerbe auf der dorsalen Seite des Ovipositors. Metafemur und Ovipositorscheide der linken Seite wurden vermessen. In der morphologischen Terminologie folgen wir Gibson (1997), die verwendeten Begriffe werden in den Abb. 1a-1d erläutert (vgl. Tab. 1). Quantitative Angaben beziehen sich auf die Gesamtheit des betreffenden Materials und sind entsprechend dem System von Goulet & Mason (1993: 64) wie folgt definiert: sehr selten <1%, selten 1-10%, gelegentlich >10-25%, manchmal >25-50%, oft >50-75%, häufig >75-90%, meist >90-99%, normalerweise >99% des vorliegenden Materials.

Eine Beurteilung der Gefährdung der einzelnen Arten in der Schweiz muss bei Parasitoiden, besonders bei streng oligophagen Arten wie *Leucospis*, naturgemäss die Gefährdung der Wirte berücksichtigen. Die Angaben richten sich deshalb weitgehend nach der Roten Liste der gefährdeten Bienen der Schweiz (Amiet, 1994). Zusätzlich wurde der Anteil rezenter Daten (Funde nach 1950) gewertet. Der Beginn für rezente Daten wurde auf einen relativ frühen Zeitpunkt festgelegt, da in den letzten drei Jahrzehnten die Sammeltätigkeit betreffend Leucospiden stark abnahm und sich mehr oder weniger auf die Anstrengungen von FA beschränkte! Die normalerweise geringe Populationsdichte sowie die spärliche Besammlung erschweren generell eine Einschätzung des eigentlichen Bestandes. Wenn jedoch eine Art früher bedeutend häufiger festgestellt wurde als in jüngster Zeit (nach 1950), so kann ein Bestandesrückgang angenommen werden (vgl. *L. gigas*).

Die Daten für das Verbreitungsbild der Wirte stützen sich auf Erhebungen von FA in folgenden Sammlungen: ETHZ, FA, NMBA, und NMBE. Die Nomenklatur der mitteleuropäischen Bienen folgt der Liste von Westrich & Dathe (1997). Alle anderen Namen werden nach Schwarz *et al.* (1996) zitiert. Die Namen von Blütenpflanzen

richten sich nach der «Flora Helvetica» von Lauber & Wagner (1996).

Für die Auswertung der Messreihen bzw. die Erstellung der Verbreitungskarten, Grafiken und Abbildungen fand die folgende Software Verwendung: DMAP, Version 6.5, 1998 (Verbreitungskarten), Adobe Photoshop, Version 5.0.2, 1998 (Beschriftung und Nachbearbeitung der Abbildungen und einiger Diagramme), SPSS, Version 9.0, 1998 (Auswertung, Diagramme).

Schliesslich sei für alle weiterführenden Angaben zur Synonymie, Morphologie und Literatur der behandelten Arten auf die Monographie der Leucospiden von Bouček (1974) sowie den CD-ROM Katalog von Noyes (1998) verwiesen.

Abkürzungen der Kantone der Schweiz

BE	Bern	SO	Solothurn
GE	Genf	TI	Tessin
GR	Graubünden	VD	Waadt
NE	Neuenburg	VS	Wallis
SH	Schaffhausen	ZH	Zürich

Abkürzungen der Sammlungen

AS	Ali Salvioni, Privatsammlung, Zürich, Schweiz
ASE	Albert Sermet, Privatsammlung, Yverdon, Schweiz
BZOL	Biologie-Zentrum des Oberösterreichischen Landesmuseums, Linz, Österreich
CS	Christian Schmid-Egger, Privatsammlung, Maulburg, Deutschland
DEI	Deutsches Entomologisches Institut, Eberswalde, Deutschland
ES	Erwin Steinmann, Privatsammlung, Chur, Schweiz
ETHZ	Eidgenössische Technische Hochschule, Entomologische Sammlung, Zürich, Schweiz
FA	Felix Amiet, Privatsammlung, Solothurn, Schweiz
FB	Frank Burger, Privatsammlung, Orlamünde, Deutschland
FNSM	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a. M., Deutschland
GC	Gilles Carron, Privatsammlung, Neuchâtel, Schweiz
GR	Gerd Reder, Privatsammlung, Flörsheim-Dalsheim, Deutschland
HB	Heinrich Bürgis, Privatsammlung, Worms, Deutschland
HT	Hansueli Tinner-Guler, Privatsammlung, Landquart, Schweiz
IW	Ingmar Wall, Privatsammlung, Mühlingen, Deutschland
MH	Martin Hauser, Privatsammlung, Urbana, Illinois, USA [Material z. Z. bei CS]
MHNG	Muséum d'histoire naturelle, Genève, Schweiz
MNHU	Museum für Naturkunde, Humboldt-Universität, Berlin, Deutschland
MSNV	Museo Civico di Storia Naturale, Venezia, Italien
MZL	Musée Zoologique, Lausanne, Schweiz
NMBA	Naturhistorisches Museum, Basel, Schweiz
NMBE	Naturhistorisches Museum, Bern, Schweiz
NMSO	Naturmuseum, Solothurn, Schweiz
NMW	Naturhistorisches Museum, Wien, Österreich

SMNS	Staatliches Museum für Naturkunde, Stuttgart, Deutschland
WA	Werner Arens, Privatsammlung, Bayreuth, Deutschland
WL	Walter Linsenmaier, Privatsammlung, Ebikon, Schweiz
ZSM	Zoologische Staatssammlung, München, Deutschland

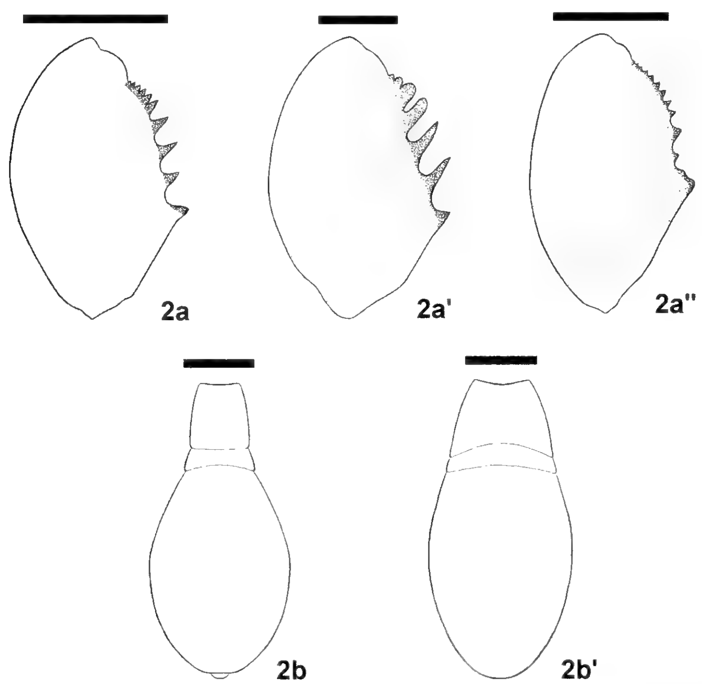
Bestimmungsschlüssel für die europäischen Arten von *Leucospis* (Massstab der Abbildungen 1 mm).[1]

1) – Metatibia dorsal rotbraun bis schwarz, höchstens in der Mitte mit feinem gelblichem Längsstreifen; basaler Zahn des Metafemurs ungefähr so lang wie folgende Zähne (Abb. 2a). ♂: Gaster im basalen Drittel stark verschmälert (Abb. 2b); ♀: Ovipositorscheide sehr kurz, nur 0.66-0.74 mal so lang wie der Metafemur . . . . *L. brevicauda*

– Metatibia dorsal gelb; basaler Zahn des Metafemurs kürzer oder länger als folgende Zähne (Abb. 2a', 2a"). ♂: Gaster im basalen Drittel breiter (Abb. 2b'); ♀: Ovipositorscheide deutlich länger, 0.90-1.93 mal so lang wie der Metafemur 2

2) – Basaler Zahn des Metafemurs kürzer als folgende Zähne (Abb. 2a'). 3

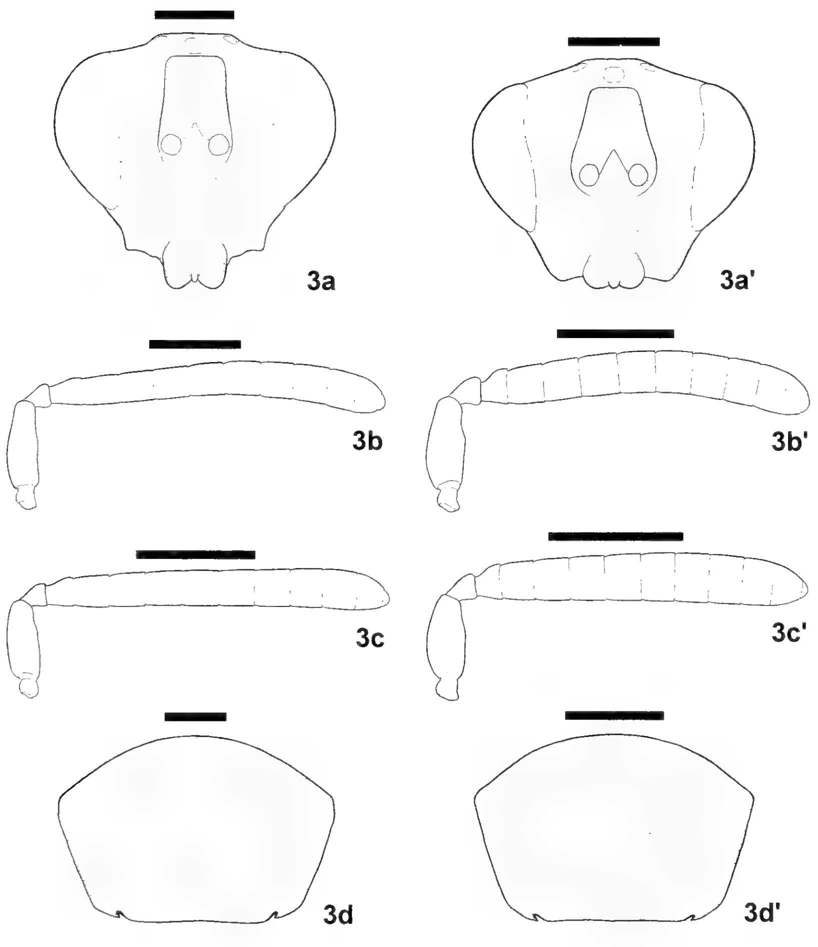
– Basaler Zahn des Metafemurs länger als folgende Zähne (Abb. 2a") 4



[1] Caleca et *al.* (1995) geben *L. miniata* Klug für die kleine Insel Lampedusa (Italien) an. Die vor allem in Nordafrika und dem Nahen Osten verbreitete Art (Bouček, 1974) wurde im Schlüssel nicht berücksichtigt. *L. miniata* ist im Habitus sehr ähnlich der orangeroten Form von *L. gigas*, sie kann aber leicht durch das gerundete, ungezähnte Dorsellum von den hier behandelten Arten unterschieden werden.

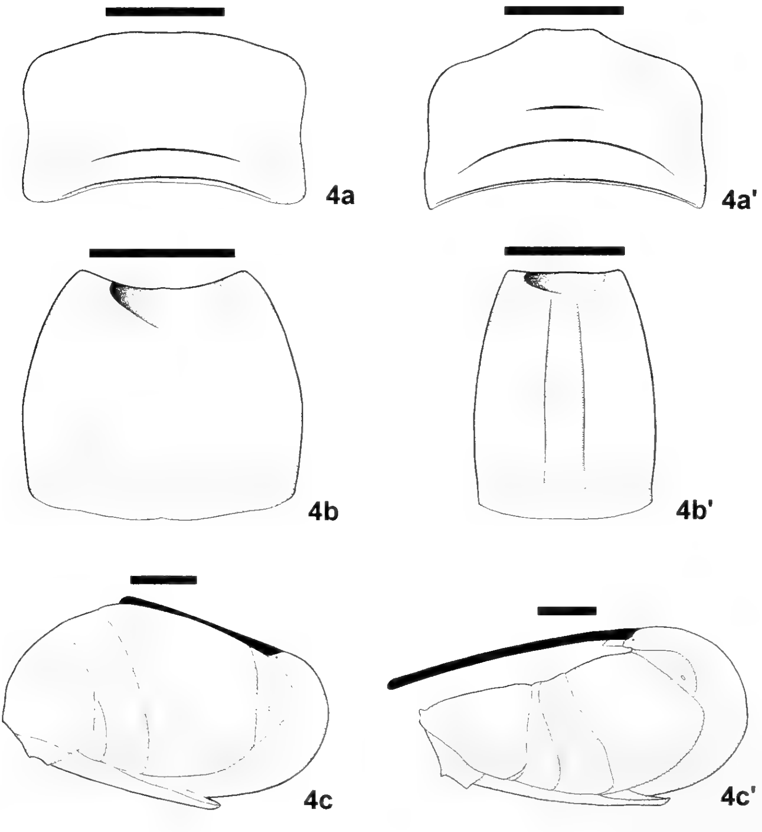
3) – Clypeus stark vorgezogen (Abb. 3a); Flagellum schlank, Glieder 2-4 beim ♀ länger als breit (Abb. 3b), beim ♂ quadratisch oder wenig länger als breit (Abb. 3c). Mesoscutum im Zentrum mit 2 gelben Flecken (Abb. 3d), manchmal diese sich gegenseitig berührend, beim ♂ oft fehlend . . . . *L. gigas*

– Clypeus mässig vorgezogen (Abb. 3a'); Flagellum gedrungener, Glieder 2-4 beim ♀ wenig kürzer als breit oder quadratisch (Abb. 3b'), beim ♂ deutlich kürzer als breit (Abb. 3c'). Mesoscutum im Zentrum mit nur 1 gelben Fleck (Abb. 3d'), beim ♂ oft fehlend . . . . *L. intermedia*



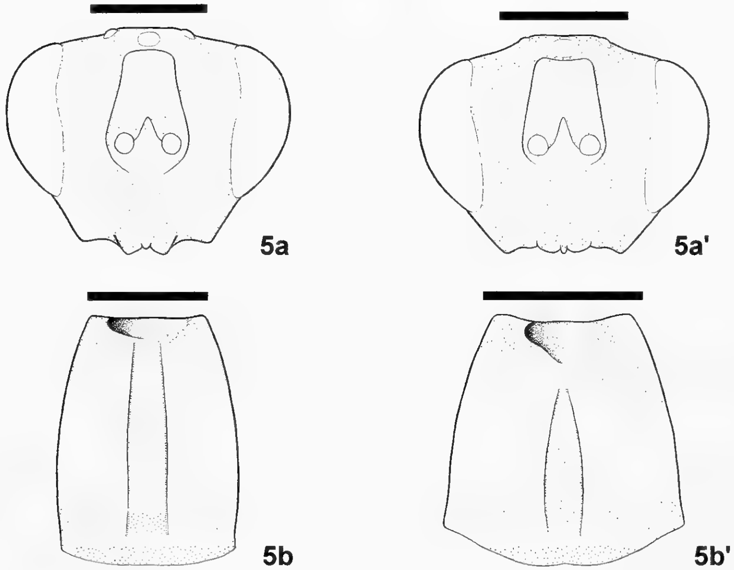
4) – Pronotum mit 2 Querkielen: einer im hinteren Viertel, der andere fast unmittelbar entlang des Hinterrandes (Abb. 4a). ♀: Ovipositor erreicht nicht das 1. Gastraltergum, dieses ohne Längsfurche und sein gelbes Querband in der Mitte stark eingeschnürt (Abb. 4b); Längsfurche des 5. Gastraltergums tief, Ovipositorscheide in Ruhelage teilweise verdeckt (Abb. 4c) . . . . *L. biguetina*

– Pronotum mit 3 Querkielen: ein kurzer ungefähr in der Mitte, gefolgt von zwei längeren im hinteren Viertel respektive fast unmittelbar entlang des Hinterrandes (Abb. 4a'). ♀: Ovipositor erreicht das 1. Gastraltergum, dieses mit Längsfurche und sein gelbes Querband in der Mitte nicht eingeschnürt (Abb. 4b'); Längsfurche des 5. Gastraltergums oberflächlich, Ovipositorscheide in Ruhelage immer ganz sichtbar (Abb. 4c') 5



5) – Clypeus deutlich vorgezogen, lateral mit aufgebogenen Lappen, welche nach unten leicht konvergieren (Abb. 5a). ♀: Längsfurche des 1. Gastraltergums an der Basis kaum verjüngt (Abb. 5b) . . . . *L. dorsigera*

– Clypeus kaum vorgezogen, mehr oder weniger verrundet und lateral nur mit fein angedeuteten Kielen (Abb. 5a'). ♀: Längsfurche des 1. Gastraltergums an der Basis deutlich verjüngt (Abb. 5b') . . . . *L. bifasciata*



Leucospis gigas Fabricius, 1793 Abb. 1a-1d, 2a', 3a-3d, 6-8, 12-14. Tab1.

Untersuchtes Material [Schweiz: alphabetisch geordnet nach Kanton, Ort; übrige Länder: alphabetisch geordnet nach Land, Provinz bzw. Region, Ort]: SCHWEIZ: ohne Fundortsangabe 2 ♀ (MNHU); «Cornet»: 1 ♀, 1867 (MHNG). BE: Bern: 3 ♀, leg./coll. M. Perty (NMBE). GE: Genève: 3 ♀, leg. Bües (ZSM); 1 ♀, 15.6.1889, 2 ♀, 20.7.1889, 5 ♀, 20.7.1889, leg./coll. F. Chevrier (MHNG). Genève, Champel: 1 ♀, [?18...], 1 ♂, 7.[?18...], 1 ♀, 18.7.[?18…], 1 ♀, 22.7.[?18…] (MHNG). GR: Brusio: 1 ♀, 31.7.-5.8.1935, leg./coll. A. Nadig (ETHZ). VD: Chamblon, Champ Muraz: 1 ♀, 1942, ex *Megachile parietina*, leg. A. Sermet (ASE). Nyon: 3 ♀, leg./coll. F. Chevrier (MHNG). VS: 1 ♀ (MSNV); 1 ♀, coll. Naumberg (DEI); 1 ♀, leg./coll. E. Frey-Gessner (NMSO); 114 ♀, leg./coll. M. Paul (NMW); 1 ♀, leg./coll. O. Schmiedeknecht (NMBE); 1 ♀, leg./coll. H. Tournier (MHNG); 6 ♀, leg. T. Steck (NMBE); 1 ♀, leg. A. Wullschlegel (NMBE). Brig: 2 ♀, 7.1914, leg./coll. A. von Schulthess (ETHZ). Euseigne: 9 ♀, 8.7.1908, 2 ♀, 5.7.1911, leg. T. Steck (NMBE); 1 ♀, 8.7.1908, 1 ♀, 25.6.1924, 1 ♀, 16.8.1929, 1 ♀, 15.7.1936, leg./coll. T. Steck (NMBA); 3 ♀, 31.7.1939, 1 ♀, 23.7.-2.8.1942, leg./coll. A. Nadig (ETHZ); 1 ♀, 2.8.1940, leg./coll. J. de Beaumont (MZL). Finges: 1 ♀, 25.7.1946, leg./coll. J. Aubert (MZL); Fully, Les Follatères: 1 ♀, 5.7.1947, leg./coll. J. Aubert (MZL). Gampel, Jeizinen: 1 ♀, 8.8.1998, an *Sedum album*, leg. H. Baur (NMBE). Martigny: 1 ♀, 7.7.1935, leg. P. Bovey (MZL); 1 ♀, 18.7.1936, 1 ♀, 25.6.1948, 1 ♀, 4.7.1948, 1 ♀, 28.6.1956, leg./coll. J. de Beaumont (MZL). Niouc: 1 ♀, 17.7.1900, leg./coll. E. Frey-Gessner (MHNG). Pfynwald: 1 ♀, 18.6.1921, 1 ♀, 2.7.1921, leg. T. Steck (NMBE); 1 ♀, 18.6.1921, 1 ♀, 3.7.1922, 1 ♀, 29.6.1924, 1 ♀, 4.7.1925, 1 ♀, 20.8.1925, 1 ♀, 21.7.1927, 2 ♀, 23.7.1927, leg./coll. T. Steck (NMBA); 6 ♀, Ende 7.1939, 1 ♀,

13.8.1941, 9 ♀, 23.7.-2.8.1942, leg./coll. A. Nadig (ETHZ). Salgesch: 1 ♀, 11.7.1885, leg./coll. M. Paul (NMW). Savièse: 1 ♀, 7.-8.1906, leg. J. Jullien, coll. V. Delucchi (ETHZ); 10 ♀, 7.1906, leg./coll. J. Jullien (MHNG). Sierre: 3 ♀, coll. A. von Schulthess (ETHZ); 1 ♀, leg./coll. Cerutti (MZL); 1 ♀, leg./coll. O. Schmiedeknecht (DEI); 3 ♀ (MHNG); 1 ♀, 6.7. (MHNG); 3 ♀, 25.6.1880, leg./coll. E. Frey-Gessner (ZSM); 1 ♀, 9.7.1884, 6 ♀, 7.1886, leg. T. Steck (NMBE); 2 ♀, 10.7.1886, leg./coll. R. Meyer-Dür (NMBE); 2 ♀, 26.2.1901, coll. A. von Schulthess (ETHZ); 2 ♀, 8.1965, leg. I. Wall (IW [nicht untersucht]). Sion: 1 ♀, leg./coll. E. Frey-Gessner (MHNG); 3 ♀, 25.6.1901, coll. A. von Schulthess (ETHZ); 1 ♀, 1906, leg. J. Jullien (MHNG); 1 ♀, 13.6.1906, leg. Suereuse (MHNG); 1 ♀, 1909, leg./coll. B. Jacob (MZL); 1 ♀, 25.6.1912, leg./coll. A. von Schulthess (ETHZ); 3 ♀, 20.6.1922, 1 ♀, 28.6.1924, leg./coll. T. Steck (NMBA). St. Niklaus: 1 ♀, 15.7.1925, 2 ♀, 16.7.1925, 1 ♀, 19.7.1927, leg./coll. E. Däniker (NMBE); 1 ♀, 19.7.1927, leg./coll. E. Däniker (WA). Stalden: 1 ♀, 26.6.1909, leg. T. Steck (NMBE); 1 ♀, 11.7.1923, 2 ♀, 14.7.1923, leg./coll. E. Däniker (NMBE); 1 ♀, 4.7.1924, leg./coll. T. Steck (NMBA). Susten: 2 ♀, 24.7.1886, leg./coll. M. Paul (NMW); 3 ♀, 13.7.1899, 1 ♀, 13.7.1899, leg./coll. B. Jacob (MZL); 1 ♀, 1.7.1900, leg./coll. E. Frey-Gessner (MHNG); Törbel: 1 ♀, 8.7.1924, leg. G. C. Krüger (ETHZ); Vex: 1 ♀, 5.7.1928, leg./coll. T. Steck (NMBA); Zeneggen: 1 ♀, 15.-29.7.1943, leg./coll. J. de Beaumont (MZL). ZH: Zürich: 1 ♀, coll. A. von Schulthess (ETHZ); 1 ♀, «Chalicodoma muraria Nest», leg./coll. A. von Schulthess (ETHZ); 1 ♀, 9.1871, leg. F. Ris, coll. A. von Schulthess (ETHZ).

Frankreich: Basses Alpes, Digne 1 ♀ (ZSM); Basses Alpes, Valensole 2 ♀ (NMBE), 2 ♀, 1 ♂ (FA); Bouches-du-Rhône, Fontvielle, Alpille's 1 ♀ (MH); Provence, Callian 1 ♀ (NMBA), 2 ♀ (NMBE); Provence, St-Jean 1 ♀ (MH). Griechenland: Hellas, Alt Korinth 1 ♀ (WA); Hellas, Antikes Samiko 1 ♀ (WA); Hellas, Epid. Limera 1 ♀ (WA); Hellas, Kalogria, Achaia 1 ♀ (WA); Hellas, Leptokoria 2 ♀ (FB); Hellas, Mavromati, Ithome 1 ♂ (WA); Hellas, Olympia, Alfios-Tal 1 ♀, 1 ♂ (WA); Peloponnes, Neapoli, Kap Malea 1 ♀ (WA). Italien: Aostatal, Nus 1 ♀, 1 ♂ (ES); Aostatal, Pondel 1 ♀ (CS); Aostatal, St. Pierre 2 ♀ (CS); Bozen 2 ♀ (NMW); Bozen, St. Pauls 1 ♀ (NMW); Sizilien, Passomartino 1 ♀ (NMBE); Triest 1 ♀ (ZSM); 1 ♀ (NMW); Triest, Conconello (Umg.) 4 ♀ (NMW); Triest, S. Primus 1 ♀ (NMW); Vinschgau, Meran 1 ♀ (DEI). Kroatien: Dalmatien, Sibenik (Adriaküste) 6 ♀, ex *Megachile hungarica* (GR); Dalmatien, Sibenik 5 ♀, ex *Megachile parietina* (GR); Krk 1 ♀ (ZSM); Krk 1 ♂ (ETHZ); Krk, Baska 4 ♀ (ZSM); Krk, Hvar 1 ♀ (ZSM); Krk, J. Hvar Jelsa 10 ♀, 4 ♂ (ZSM); Krk, Malinska 5 ♀ (ZSM); Rijeka 2 ♀ (ETHZ). Malta: 3 ♀ (NMBE). Österreich: Tirol, Klobenstein 1 ♀ (NMW); Tirol, «Larche» 1 ♀ (NMW). Tunesien: Sbeitla 1 ♀ (NMBE). Türkei: Kayseri, Göreme 1 ♀ (CS).

Diagnose ♀: Körper schwarz mit folgenden Teilen gelb [bei manchen südeuropäischen und nordafrikanischen Individuen leuchtend orangerot]: Gesicht beiderseits der Scroben mit je einem Fleck (Abb. 3a); Scapus ausser an Basis und Apex, manchmal auch dorsal dunkel; Flagellumglieder 1-3 an der Basis häufig leicht rötlich; Pronotum vorne mit langem, hinten mit etwas kürzerem Querband, oder das Sklerit vollständig eingerahmt; Mesoscutum mit 2 Flecken zentral und 2 länglichen Flecken lateral (Abb. 3d); Scutellum am Hinterrand mit in der Mitte stark eingeschnürtem Querband; Mesepisternum selten mit einem Fleck; Metapleuron vollständig hell; Metacoxa dorsal mit Basalfleck, ventral gelegentlich mit Apikalfleck; Pro- und Mesofemur apikal zu 2/3 bis 1/4; Aussenseite des Metafemurs, ausser einem dunklen Fleck und den Zähnen (Abb. 2a'); Tibien und Tarsen, nur Metatibia ventral dunkel; Gastralterga 1, 4 und 5 mit breiten Querbändern, welche in der Mitte unterbrochen sind; Tergum 7 lateral mit länglichen Flecken.

Clypeus stark vorgezogen (Abb. 3a); Flagellum schlank, leicht keulenförmig, Glieder 2-4 länger als breit (Abb. 3b); Pronotum mit 2 Querkielen: einer im hinteren Viertel, der andere fast unmittelbar entlang des Hinterrandes (ähnlich *L. biguetina*, Abb. 4a); Dorsellum am Hinterrand mässig ausgerandet, die beiden Zähne mehr oder

weniger deutlich; basaler Zahn des Metafemurs kürzer als folgende Zähne (Abb. 2a'); Längsfurche des 1. Gastraltergums an der Basis leicht verjüngt; Längsfurche des 5. Tergums oberflächlich, Ovipositorscheide in Ruhelage immer ganz sichtbar (Abb. 1d); Ovipositorscheide 0.95-1.46 mal so lang wie der Metafemur (Abb. 12), reicht bis ungefähr zur Hälfte, zum basalen Viertel oder zur Basis des 1. Gastraltergums (vgl. Variabilität ♀).

Körperlänge 7.0-17.2 mm (Abb. 13), Kopfbreite 2.15-3.95 mm (Abb. 14).

D i a g n o s e ♂: Gelbe Zeichnungselemente oft reduziert, die Flecken im Gesicht und im Zentrum des Mesoscutums oft fehlend; Querbänder auf dem Gaster durchgehend.

Flagellum etwas gedrungener, Glieder 2-4 quadratisch oder wenig länger als breit (Abb. 3c). Form des Gasters ähnlich *L. dorsigera* (Abb. 2b').

Körperlänge 11.2-14.5 mm (Abb. 13), Kopfbreite 2.85-3.40 mm (Abb. 14).

V a r i a b i l i t ä t ♀: Aufgrund des Verhältnisses Ovipositorscheide- zu Metafemurlänge (O/M) können drei Formen unterschieden werden (Abb. 12), welche zusätzlich bis zu einem gewissen Grad in der Zeichnung und der Grösse (Abb. 13, 14) variieren. Die Formen 'A' und 'B' mit kurzer (O/M = 0.95-1.18, n = 79) respektive langer (O/M = 1.30-1.46, n = 18) Ovipositorscheide treten häufig zusammmen in mittel- und südeuropäischen Populationen auf. Im Wallis kommt hingegen nur eine dritte Form vor, welche in der Länge der Ovipositorscheide (O/M = 1.16-1.30, n = 123) eine intermediäre Stellung einnimmt. Die Unterschiede der Walliser Population zu den beiden anderen Formen sind hoch signifikant (ANOVA mit Dunnett T3-Test, $F = 992.887$, $n = 220$, $p < 0.001$). Die Formen 'A' und 'B' wurden schon relativ früh erkannt und als separate Arten unter eigenen Namen beschrieben (Klug, 1814). Nach Bouček (1974) sind diese aber eindeutig als Synonyme von *L. gigas* zu werten.

V e r b r e i t u n g : Paläarktisch, östlich bis China (Bouček, 1974); in Mitteleuropa aus allen Ländern nachgewiesen (vgl. Bouček, 1959; Madl, 1989; Schletterer, 1890). In der Schweiz wurde die Art ausser im Mittelland bei Bern und Zürich und am Jurasüdfuss bei Yverdon vor allem im Süden (Genferseebecken, GR, VS) gefunden (Abb. 6). Nach 1950 wurde *L. gigas* nur noch sehr selten (0.4% der Daten, 16% der Fundpunkte auf der Verbeitungskarte) und ausschliesslich im Wallis gesammelt. Die Verbreitung stimmt recht gut mit derjenigen der potentiellen Wirte überein, wobei diese in der Schweiz weiter verbreitet sind (Nordschweiz, GE, TI, GR) (Abb. 6).

H ö h e n v e r b r e i t u n g : von 375 bis 1505 m ü. M. (Abb. 6).

G e f ä h r d u n g : in der Nordschweiz wahrscheinlich ausgestorben, in der Südschweiz gefährdet und in der ganzen Schweiz stark gefährdet. Von den potentiellen Wirtsarten wird *Megachile parietina* (Geoffroy) in der Roten Liste (Amiet, 1994) für die Nordschweiz als vom Aussterben bedroht, für die Südschweiz und für die ganze Schweiz als gefährdet eingestuft. *M. pyrenaica* Lepeletier, welche vor allem in den Alpen, selten im Jura und im Mittelland vorkommt, gilt als nicht gefährdet. Die Beurteilung der Gefährdung von *M. parietina* trifft ebenfalls recht gut auf *L. gigas* zu. Allerdings ist die Art in der Nordschweiz, wo sie nach Sulzer (1776) und Fuessly (1783) z. B. im Kanton Zürich mehr oder weniger regelmässig auftrat, wohl überall ausgestorben. Zudem ist sie im Wallis im Rhonetal stark zurückgegangen. Aufgrund

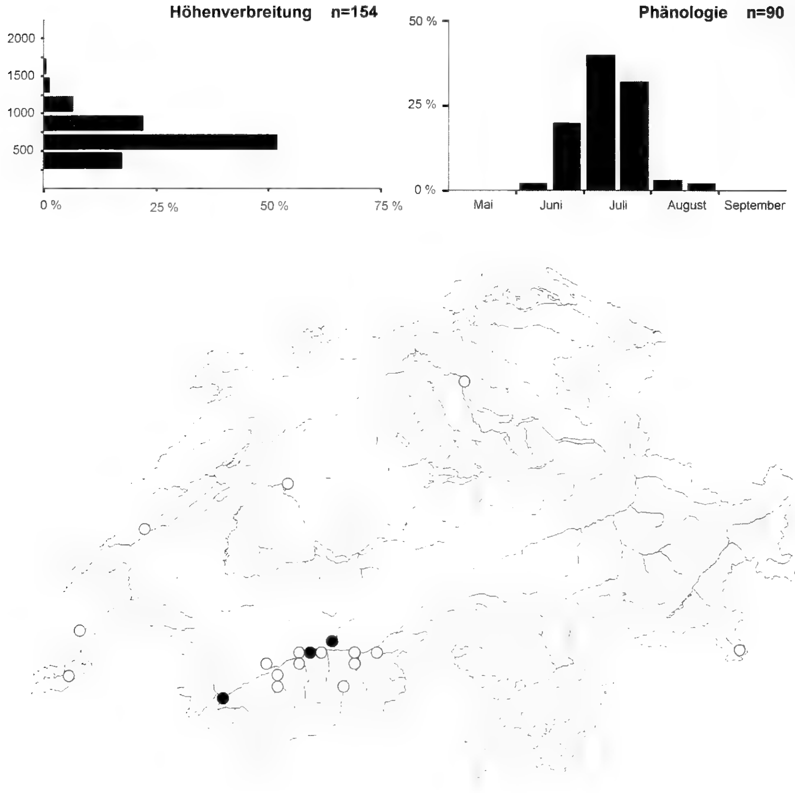


Abb. 6, *L. gigas*: Höhenverbreitung, Phänologie und Verbreitung in der Schweiz; ● Funde nach 1950, ○ Funde vor 1951, potentielle Wirte (Auswertung von 100 Datensätzen von *Megachile parietina* und *M. pyrenaica*).

der Daten war die Art dort früher wahrscheinlich verbreitet und relativ häufig. Gegenwärtig ist sie aber nur noch von einer einzigen Stelle bei Jeizinen bekannt. Vor diesem Hintergrund muss *L. gigas* für die gesamte Schweiz als stark gefährdet eingestuft werden.

B i o l o g i e : Zu den Wirten werden die folgenden Angaben gemacht, welche als gesichert gelten können: *Megachile parietina* (Amiet, Baur, Forster und Zettel, pers. Beob. an Nestern im Wallis; Fabre, 1886 sub «Chalicodome des murailles» oder «Chalicodome des galets»; Bouček, 1970, Fahringer, 1922, Giraud & Laboulbène, 1877 und Schletterer, 1890 sub *Chalicodoma muraria*); *M. pyrenaica* (Fabre, 1886 sub «Chalicodome des hangars»; Fahringer, 1922 sub *Chalicodoma*), *M. sicula* (Rossi) (Schletterer, 1890 sub *Chalicodoma*; Bürgis, 1995). Ferner wurden die

ABB. 7: Weibchen von *L. gigas* schlüpft aus einem Nest von *Megachile parietina* von Sibenik (Kroatien). Daneben die Exuvie und die Imago der ebenfalls parasitischen *Anthrax ?binotatus* Wiedemann (Diptera: Bombyliidae) (Foto G. Reder).

folgenden Exemplare mit zuverlässigen Wirtsangaben untersucht: FRANKREICH: Korsika, Calvi (Umgebung), Stareso, 24.9.1991, ex *M. sicula* 1 ♀, e. p. 11.-13.6.1993, 1 ♀, e. p. 1994, leg. H. Bürgis (HB). KROATIEN: Dalmatien, Sibenik (Adriaküste) 6 ♀, e. p. 14.-22.5.1998, ex *M. hungarica* (Mocsáry), 5 ♀, e. p. 22.-29.5.1998, ex *M. parietina*, leg. G. Reder (GR). SCHWEIZ: VD, Chamblon, Champ Muraz 1 ♀, 1942, ex *M. parietina*, leg. A. Sermet (ASE). ZH, Zürich 1 ♀, ex *M. parietina*, leg./coll. A. von Schulthess (ETHZ).

Die Nennung weiterer Wirte von *L. gigas* geht zumeist auf eine einzige, oft recht alte Quelle zurück. So erwähnt Fahringer (1922) den Schlupf von mehreren *Osmia bicornis* (Linnaeus) und einem Exemplar von *L. gigas* aus einem verlassenen Nest von *M. parietina*. Da *L. gigas* bis zu drei Jahren überliegen kann (Bürgis, 1995), ist nicht auszuschliessen, dass die Entwicklung zuvor an *M. parietina*, und nicht an *O. bicornis*, stattfand. Mann fand «in Corsica einen über nussgrossen, kugeligen Bau, aus Thon und Sandkörnern hergestellt und an einem Zweige von Cystus salviaefolius befestigt» woraus *Odynerus trifasciatus* Fabricius (Vespidae), *Osmia 'coerulea'* [= ?*O. caerulescens* (Linnaeus)] und *L. gigas* schlüpften (Schletterer, 1890: 11). Hier

ABB. 8: Ausschnitt aus dem Habitat von *L. gigas* bei Jeizinen im Wallis (Schweiz) (Foto B. Baur).

Osmia als Wirt anzunehmen, ist zwar naheliegend, aber möglicherweise irreführend. So passt die Beschreibung des «Bau» vorzüglich auf das Nest von *M. sicula*, in diesem Fall der wahrscheinlichere Wirt. Der Parasitoid könnte *M. sicula* zu einem frühen Zeitpunkt attackiert haben, und dann, nach Jahren des überliegens, gleichzeitig mit der *O. caerulescens* geschlüpft sein, welche in der Zwischenzeit die verwaisten Zellen für sich benutzte. Die Wirtsangabe *Anthophora garrula* (Rossi) (Fahringer, 1922 sub *Podalirius*) bedarf der Bestätigung, diejenige von *Vespula vulgaris* (Linnaeus) (Rondani, 1873) ist äusserst zweifelhaft.

Brutparasiten (*Coelioxys*, *Stelis*) werden gelegentlich als Wirte von *Leucospis* erwähnt, konnten aber bisher nicht schlüssig bestätigt werden. Bouček (1974) berichtet lediglich von einem Exemplar von *L. gigas*, das in Frankreich zusammen mit *Coelioxys quadridentata* (Linnaeus) [= *C. conica* (Linnaeus)] gezogen wurde. Amiet (pers. Beob.) beobachtete jedoch im Juli in Sambiase, Kalabrien, Italien, wie ein Exemplar von *L. gigas* mehrmals immer wieder an der gleichen Stelle das Nest einer *Megachile* sp. (*parietina* oder *sicula*) anstach. Die Untersuchung des Nestes ergab vier Zellen, eine verschimmelte, zwei besetzt mit mehreren Larven von ?*Stelis nasuta* (Latreille) und eine mit einer fertig entwickelten *Megachile*-Larve. Die *Leucospis* setzte die Spitze des Ovipositors genau über der letztgenannten Zelle an.

Fabre (1886) schildert in seinem Aufsatz über die *Leucospis* eingehend das Verhalten von *L. gigas*. Eine kurze Zusammenfassung über das Eiablageverhalten sowie die Ontogenie einschliesslich Abbildungen des Eis und der Larvenstadien findet sich in Clausen (1940). Bürgis (1995) berichtet, dass *L. gigas* bis zu mehreren Jahren im Nest von *Megachile sicula* ausharren könne. Entgegen der verbreiteten Annahme (z. B. in Jacobs & Renner, 1998), wonach die fertig entwickelte Wespe auf

die Hilfe eines zuvor schlüpfenden Wirtes, welcher einen Ausgang freimache, angewiesen sei, befreiten sich alle Exemplare selbständig aus dem Nest (Bürgis, 1995). Ferner konnte Reder (pers. Beob.) mehrere Exemplare von *L. gigas* beim Schlupf aus Nestern von *M. parietina* (Abb. 7) bzw. *M. hungarica* beobachten. Auch in diesem Fall haben alle Parasitoide mit Hilfe der Mandibeln scheinbar mühelos das Nest selbständig verlassen.

Imagines erscheinen von Juni bis August (Abb. 6) und werden meist an xerothermen Standorten wie Steppen- und Trockenrasen (Abb. 8) angetroffen, wo sie in unruhigem, raschem Flug das Gelände nach Nestern der Wirte absuchen. Einzelne Exemplare konnten auf Blüten von *Allium sphaerocephalon* Linnaeus (Liliaceae) (Forster, pers. Beob.) und *Sedum album* Linnaeus (Crassulaceae) (vgl. Material) beobachtet werden. Nach Ansicht verschiedener Autoren (Berland, 1934a; Bytinski-Salz, 1963) vermehrt sich *L. gigas* in Europa vor allem parthenogenetisch (thelytok), da hier Männchen nur selten gefunden werden. Dies scheint auch für die Populationen in der Schweiz zuzutreffen, denn unter den insgesamt 281 untersuchten Exemplaren befindet sich nur ein einziges Männchen aus der Nähe von Genf.

Leucospis intermedia Illiger, 1807 Abb. 3a'-3d', 9, 12-14

Untersuchtes Material: SCHWEIZ: GR: Brusio: 2 ♂, 31.7.-5.8.1935, leg./coll. A. Nadig (ETHZ). Grono: 3 ♀, 7.1887, leg. T. Steck (NMBE); 1 ♀, 21.8.1934 (NMBA). Roveredo: 1 ♂, 20.7.1928, leg./coll. A. Nadig (ETHZ); 1 ♀, 7.8.1935, leg./coll. T. Steck (NMBA). VD: Buchillon: 1 ♀, 17.7.1930, leg. P. Bovey (ETHZ). Nyon: 1 ♂, leg./coll. F. Chevrier (MHNG). VS: ohne Fundortsangabe 1 ♀, leg. A. Wullschlegel (NMBE); 1 ♂, leg./coll. E. Frey-Gessner (NMW); 1 ♀, leg./coll. H. Tournier (MHNG). Aven: 1 ♀, 28.5.1992, leg./coll. F. Amiet (NMSO). Branson: 2 ♂, 30.5. (MHNG); 1 ♂, 23.6.1964, 1 ♀, 29.7.1964, leg./coll. J. de Beaumont (MZL). Euseigne: 1 ♂, 5.7.1911, leg. T. Steck (NMBE); 2 ♀, 31.7.1939, leg./coll. A. Nadig (ETHZ). Evolène: 1 ♂, 14.7.1911, leg. T. Steck (NMBE). Fully, Les Follatères: 1 ♂, 1929 (MHNG); 2 ♀, 11.7.1933, 1 ♀, 21.7.1933, 1 ♂, 1 ♀, 27.6.1942, leg. P. Bovey (MZL); 2 ♂, 1 ♀, 12.6.1944, 1 ♀, 19.5.1948, leg./coll. A. Nadig (ETHZ); 1 ♀, 14.6.1951, leg./coll. J. Aubert (MZL); 1 ♀, 29.7.1964, leg./coll. J. de Beaumont (MZL). Grimentz: 1 ♀, 27.7.-12.8.1944, leg./coll. J. de Beaumont (MZL). Val d'Hérens: 1 ♂, 26.6.1894, leg./coll. M. Paul (NMW). Martigny: 1 ♀, leg./coll. B. Jacob (MZL); 1 ♂, 1 ♀, 1.-4.6.1875, 1 ♀, 7.-8.6.1875, leg./coll. E. Frey-Gessner (ZSM); 1 ♂, 5 ♀, 15.6.1889, leg. T. Steck (NMBE); 1 ♀, 5.7.1933, leg./coll. J. de Beaumont (MZL). Mazembroz: 1 ♂, 14.5.1934, leg. P. Bovey (ETHZ); 1 ♂, 18.5.1975, 1 ♂, 6.6.1976, 1 ♂, 13.8.1977, 2 ♂, 2.6.1988, leg. F. Amiet (FA). Niouc: 2 ♀, 12.8.1908, leg. T. Steck (NMBE). Ried bei Mörel, Riederalp: 1 ♀, 16.7.1921, leg./coll. E. Däniker (NMBE). Sierre: 1 ♂, 3 ♀, coll. A. von Schulthess (ETHZ); 1 ♀, leg./coll. A. von Schulthess (ETHZ); 1 ♂, leg./coll. O. Schmiedeknecht (NMW); 1 ♂, leg./coll. O. Schmiedeknecht (MNHU); 1 ♂, 16.7.1880, ex *Megachile* sp., leg./coll. E. Frey-Gessner (MHNG); 1 ♂, 9.7.1884, leg./coll. A. von Schulthess (ETHZ); 1 ♂, 22.7.1884, 1 ♀, 7.1886, leg. T. Steck (NMBE); 1 ♂, 24.6.1885, leg./coll. M. Paul (MHNG); 1 ♂, 27.6.1886, 3 ♀, 1887, leg. M. Paul, coll. A. von Schulthess (ETHZ). Sion: 1 ♀, leg./coll. F. Chevrier (MHNG); 1 ♂, 8.7.1884, leg. T. Steck (NMBE); 1 ♀, 9.1912 (NMBA). St. Niklaus: 1 ♀, 19.7.1927, leg./coll. E. Däniker (NMBE). Stalden: 1 ♂, 26.6.1909, 1 ♂, 1 ♀, 27.6.1909, 3 ♂, 2 ♀, 28.6.1909, leg. T. Steck (NMBE). Vex: 2 ♂, 21.6.1935, leg./coll. T. Steck (NMBA). Zeneggen: 1 ♀, 20.7.1986, leg. F. Amiet (FA).

FRANKREICH: Py-Montet 1 ♂ (MH); Tence 1 ♀, ex *Osmia emarginata* (MHNG). GRIECHENLAND: Hellas, Kallogria, Achaia 2 ♀ (WA); Peloponnes, Blafonisoa 1 ♀ (WA). ITALIEN: Aostatal, W Arvier 1 ♂ (CS); Aostatal, Sarre 1 ♀ (CS); Aostatal, St. Pierre 1 ♀ (CS); Bozen 2 ♀, 1 ♂ (NMW); Bozen 2 ♀, 2 ♂ (ETHZ); Puglia, Mte. Gargano, NW M. S. Angelo 1 ♀ (ETHZ); Sizilien, Siracusa 1 ♀ (NMBE); Vinschgau, Latsch 1 ♀ (ES). KROATIEN: Dalmatien,

Split 6 ♀ (NMW); Krk 2 ♀ (ETHZ); Krk, Hvar 2 ♀ (ZSM); Krk, J. Hvar Jelsa 1 ♀ (ZSM). ÖSTERREICH: Kärnten, Villach 1 ♀ (NMW); Tirol, «Larche» 1 ♀ (NMW).

Diagnose ♀ ähnlich der von *L. gigas*, aber: Flagellumglieder 1-3 nie rötlich; Pronotum vorne mit kurzem, hinten mit langem Querband (ähnlich *L. dorsigera*, Abb. 4a'), oft das Sklerit vollständig eingerahmt; Mesoscutum mit nur 1 Fleck zentral; Propodeum selten mit je einem kleinen Fleck lateral; Querband auf Gastraltergum 4 manchmal kaum unterbrochen.

Clypeus mässig vorgezogen (Abb. 3a'); Flagellum gedrungener als bei *L. gigas*, fast zylindrisch, Glieder 2-4 wenig kürzer als breit oder quadratisch (Abb. 3b'); Längsfurche des 1. Gastraltergums normalerweise nicht verjüngt; Ovipositorscheide länger, 1.46-1.93 mal so lang wie der Metafemur (Abb. 12), reicht meist mindestens bis zum Hinterrand des Scutellums, oft bis zu dessen Mitte.

Körperlänge 4.5-12.3 mm (Abb. 13), Kopfbreite 1.45-3.10 mm (Abb. 14).

Diagnose ♂: Gelbe Zeichnungselemente oft reduziert, der Fleck im Zentrum des Mesoscutums oft fehlend; Querbänder auf dem Gaster durchgehend.

Flagellum etwas gedrungener, Glieder 2-4 deutlich kürzer als breit (Abb. 3c'). Form des Gasters ähnlich *L. dorsigera* (Abb. 2b').

Körperlänge 6.8-10.2 mm (Abb. 13), Kopfbreite 2.05-2.85 mm (Abb. 14).

Verbreitung: Paläarktisch, östlich bis Tadschikistan (Bouček, 1974); in Mitteleuropa aus allen Ländern nachgewiesen (vgl. Bouček, 1959; Madl, 1989, 1990; Schletterer, 1890). In der Schweiz ist die Art auf das Wallis, das Genferseegebiet und die Alpensüdtäler beschränkt (Abb. 9). Nach 1950 wurde *L. intermedia* nur noch gelegentlich (19% der Daten, 22% der Fundpunkte auf der Verbreitungskarte) und ausschliesslich im Wallis gesammelt. Die Verbreitung stimmt, mit Ausnahme des Genferseebeckens, recht gut mit derjenigen des potentiellen Wirtes überein, wobei dieser in der Schweiz weiter verbreitet ist (Mittelland, Alpen) (Abb. 9).

Höhenverbreitung: von 290 bis 1925 m ü. M. (Abb. 9).

Gefährdung: nicht gefährdet. Der potentielle Wirt *Osmia mustelina* Gerstäcker hat keinen Eingang in die Rote Liste (Amiet, 1994) gefunden und gilt in der Schweiz als nicht gefährdet.

Biologie: Als Wirt wird von verschiedenen Autoren bisher nur *Osmia emarginata* Lepeletier angegeben (z. B. Berland, 1934b für Frankreich; Bouček, 1959 für Tschechien; Giraud, 1858 für Österreich; Madl, 1990 für Deutschland). Allerdings werden in jüngerer Zeit die Populationen östlich von Frankreich als eigene Art, *O. mustelina*, aufgefasst. Daher kommt als Wirt von *L. intermedia* in der Schweiz vor allem diese *Osmia*-Art in Frage. Ferner wurden die folgenden Exemplare mit Wirtsangabe untersucht: FRANKREICH: Haute-Loire, Tence 1 ♀, 16.7.1925, «parasite d'O. emarginata» (MHNG); SCHWEIZ: VS, Sierre 1 ♂, 16.7.1880, «nid de Megachile No. 9320, e. p. 4. 1881», leg./coll. E. Frey-Gessner (MHNG); SPANIEN: Soria, Beraton 1 ♀, 22.6.1994, an Nest von *O. emarginata*, leg. F. Amiet (FA). Die Wirtsangabe von Frey-Gessner bedarf der Bestätigung!

Imagines erscheinen von Mai bis August (Abb. 9) und werden meist an xerothermen Standorten wie Steppen- und Trockenrasen angetroffen, wo sie in raschem Flug das Gebiet nach Nestern ihrer Wirte absuchen. Frühere Vermutungen, dass sich *L. intermedia* in Europa vor allem parthenogenetisch (thelytok) fortpflanze (Bouček, 1964), konnten nicht bestätigt werden, da Männchen überall recht zahlreich gefunden wurden.

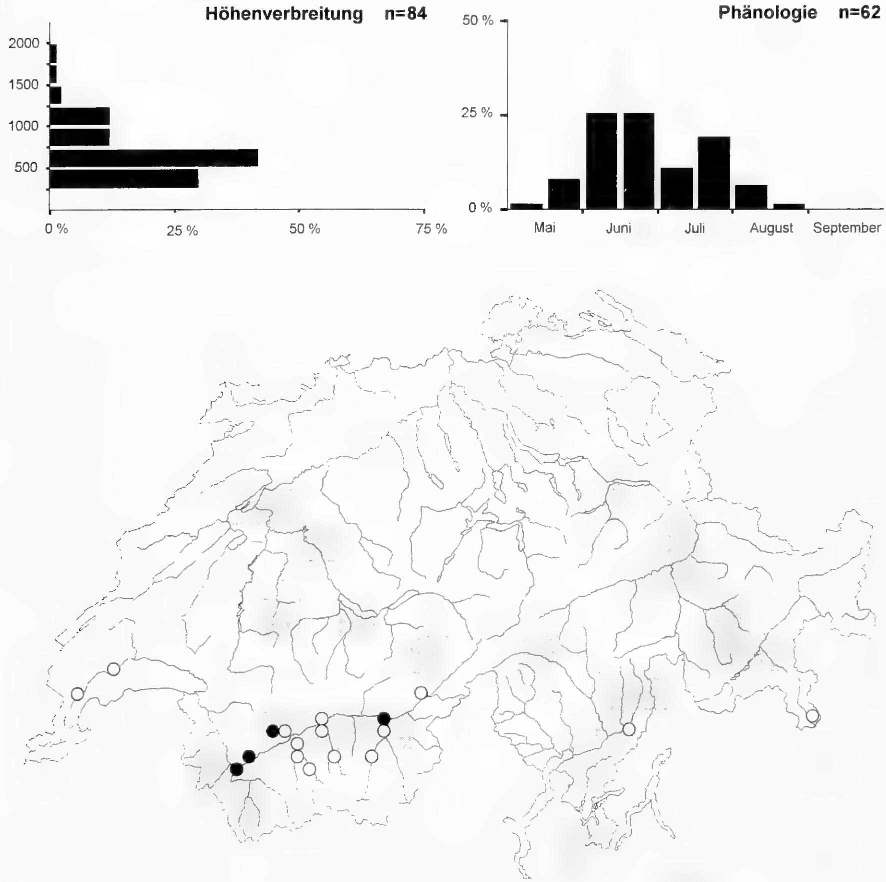


ABB. 9, *L. intermedia*: Höhenverbreitung, Phänologie und Verbreitung in der Schweiz; ● Funde nach 1950, ○ Funde vor 1951, potentieller Wirt (Auswertung von 38 Datensätzen von *Osmia mustelina*).

Leucospis dorsigera Fabricius, 1775 Abb. 2b', 4a'-4c', 5a, 5b, 10, 12-14

Untersuchtes Material: Schweiz: ohne Fundortsangabe 1 ♂, leg. Morawitz, coll. Gerst. (MNHU). BE: Bätterkinden: 1 ♀, 25.7.1887, leg./coll. T. Steck (NMBA). Bern: 2 ♀, leg./coll. M. Perty (NMBE); 1 ♀, 1.8.1897, leg. T. Steck (NMBE). Bern, Kirchenfeld: 1 ♂, 9.6.1922, leg./coll. T. Steck (NMBA). Biel: 1 ♀, 29.7.1888, leg./coll. T. Steck (NMBA). Lyss: 1 ♀, 26.6.1908, leg. T. Steck (NMBE); 1 ♀, 26.8.1923, leg./coll. T. Steck (NMBA). La Neuveville: 1 ♀, 13.7.1897, leg./coll. B. Jacob (MZL). GE: l'Allondon: 1 ♀, 29.6.1957, 2 ♀, 20.6.1959, leg./coll. Steffen (MHNG). Genève, Champel: 1 ♀, 17.9.[?18...] (MHNG). Genève, Corsier: 1 ♀, 14.7.1985, leg./coll. Steffen (MHNG). Russin: 1 ♀, 6.8.1995, leg. F. Amiet (FA). Satigny, Peney: 1 ♀, 30.5.1875 (MHNG); 1 ♂, 21.6.1875 (MHNG); 1 ♀, 7.1875 (MHNG); 1 ♀, 1.7.1875 (MHNG). GR: Grono: 4 ♀, 7.1885, leg. T. Steck (NMBE); 1 ♀, 27.6.1921, 2 ♀, 30.6.1923, 1 ♀, 19.8.1924, leg./coll. T. Steck (NMBA). Klosters: 1 ♀ (ETHZ). Landquart: 1 ♂, 8.6.1996, 1 ♀, 14.6.1996, an *Osmia adunca* Brutplatz, leg. H. Tinner-Guler (HT). Mesocco: 1 ♀, 14.7.1927, leg./coll. T. Steck (NMBA). Roveredo: 1 ♀, 19.8.1924, 1 ♀, 18.-20.6.1926,

1 ♀, 20.7.1928, 1 ♂, 2 ♀, 23.7.-3.8.1933, 1 ♀, 17.8.1949, leg./coll. A. Nadig (ETHZ); 1 ♂, 1 ♀, 18.8.1934, 1 ♂, 5.8.1935, 1 ♀, 7.8.1935, leg./coll. T. Steck (NMBA). Roveredo, S. Vittore: 1 ♀, 3.-10.8.1942, leg./coll. A. Nadig (ETHZ). NE: Auvernier: 1 ♀, 7.9.1907, leg./ coll. B. Jacob (MZL). SH: Merishausen: 1 ♀, 9.8.1999, leg./coll. G. Bächli (NMBC). SO: Dornach: 1 ♀, 3.8.1995, leg./coll. F. Amiet (FA). Solothurn: 1 ♀, 4.8.1995, leg./coll. F. Amiet (FA). TI: Acquarossa: 1 ♀, 9.-10.1951, leg./coll. Lautner (NMBA). Agno: 2 ♂, 1 ♀, 15.7.1944, leg./coll. J. de Beaumont (MZL). Bignasco: 1 ♀, 1905, leg. T. Steck (NMBE). Capolago: 1 ♀, 12.7.1944, leg./coll. J. de Beaumont (MZL). Chiasso, Pedrinate: 1 ♀, 16.8.1997, leg. F. Amiet (FA); Claro: 1 ♀, 6.8.1996, leg. A. Salvioni (AS). Gordola: 1 ♂, 26.7.1933, leg./coll. A. Nadig (ETHZ). Losone: 1 ♀, 30.6.-2.7.1959, leg./coll. J. de Beaumont (MZL). Maroggia: 1 ♂, 8.[?19...], 1 ♀, 27.8.[?19…], 1 ♀, 8.1919, leg. G. C. Krüger, coll. A. von Schulthess (ETHZ). Minusio: 1 ♂, 4 ♀, 30.6.1953, 1 ♀, 30.6.1953, an Apiaceae, 2 ♀, 7.7.1953, leg./coll. A. Nadig (ETHZ). Novaggio: 1 ♀, 6.1911, coll. A. von Schulthess (ETHZ); 1 ♂, 26.6.1920, leg./coll. T. Steck (NMBA). VD: Bonvillars, 1 ♀, 3.8.1981, leg./coll. Steffen (MHNG). Commugny: 1 ♀, 24.7.1949, 1 ♀, 1.8.1954, 1 ♀, 21.7.1948, 1 ♀, 6.8.1950, 1 ♀, 19.7.1949, 1 ♀, «Eté» 1946, 1 ♀, 24.7.1955, leg./coll. Steffen (MHNG). Cudrefin: 1 ♀, 15.8.1926, leg./coll. T. Steck (NMBA). La Sauge: 1 ♀, 10.8.1959, leg./coll. J. de Beaumont (MZL). VS: 1 ♂, coll. A. von Schulthess (ETHZ); 1 ♂, coll. H. Tournier (MHNG). Chandolin: 1 ♀, 5.7.1968 (MHNG); 1 ♀, 7.7.1968 (MHNG). Euseigne: 1 ♀, 3.7.1897, 1 ♀, 6.8.1933, leg. T. Steck (NMBE); 1 ♀, 27.6.1924, 1 ♀, 6.8.1932, 1 ♀, 8.8.1932, leg./coll. T. Steck (NMBA); 1 ♂, 25.-26.7.1939, 1 ♂, 12.6.1948, leg./coll. A. Nadig (ETHZ). Fully, Les Follatères: 1 ♂, 23.7.-2.8.1942, leg./coll. A. Nadig (ETHZ). Hohtenn: 1 ♀, 29.9.1987, 1 ♂, 15.9.1991, leg. F. Amiet (FA); 1 ♀, 26.7.1994, leg. S. Ungricht (ETHZ). Leuk, Platten, Rotten: 1 ♀, 10.8.1997, leg. B. Merz (ETHZ). Martigny: 1 ♂, 15.6.1889, 1 ♂, 15.6.1889, leg. T. Steck (NMBE); 1 ♂, 18.7.1936, 1 ♀, 29.6.1946, leg./coll. J. de Beaumont (MZL). Mazembroz: 1 ♀, 6.6.1976, leg. F. Amiet (FA). Mörel: 1 ♀, 1.8.1939, leg./coll. A. Nadig (ETHZ). Niouc: 1 ♂, 12.7.1908, leg. T. Steck (NMBE). Pfynwald: 1 ♂, 28.8.1885, leg. M. Paul, coll. A. von Schulthess (ETHZ); 1 ♀, 9.7.1975, leg. F. Amiet (FA); 1 ♀, 15.7.1977, leg. F. Amiet (FA); 1 ♀, 1989, leg. M. Paul, coll. A. von Schulthess (ETHZ); 3 ♀, 13.8.1997, leg. B. Merz (ETHZ). Sierre: 2 ♀, coll. A. von Schulthess (ETHZ); 1 ♂, 7.7.[?18...], 1 ♀, 1.8.[?18…] (MHNG); 1 ♀, 20.7.1884, leg. T. Steck (NMBE); 3 ♀, 1887, 2 ♀, 7.9.1887, leg. M. Paul, coll. A. von Schulthess (ETHZ). Sierre, Le Glarey: 1 ♀, 12.7.1905, leg. J. Jullien (MHNG). Sion: 1 ♀, 25.6.1912, leg./coll. A. von Schulthess (ETHZ). St. Niklaus: 1 ♀, 15.7.1925, leg./coll. E. Däniker (NMBE). Susten: 1 ♀, leg./coll. B. Jacob (MZL); 1 ♀, 7.8.1887, leg. M. Paul, coll. A. von Schulthess (ETHZ). ZH: Zürich: 1 ♀, coll. A. von Schulthess (ETHZ); 1 ♀, 9.1870, leg. F. Ris, coll. A. von Schulthess (ETHZ). Zürich, Albisgüetli: 1 ♀, 31.7.1995, an *Daucus carota*, leg. S. Ungricht (ETHZ).

DEUTSCHLAND: Baden-Württemberg, Freiburg i. B. 1 ♀, 2 ♂ (ETHZ); Baden-Württemberg, Kaiserstuhl 4 ♀, 1 ♂ (ETHZ); Bayern, Dudenhofen 1 ♂ (MH); Bayern, Eichstätt 2 ♀ (ZSM); Bayern, Nürnberg, Laufamholz 1 ♀, 2 ♂ (ZSM); Hessen, Flörsheim-Dalsheim 1 ♀ (GR); Landau 1 ♀ (ZSM); Thüringen, Frankenhausen, Kyffhäusern 2 ♀ (DEI). FRANKREICH: Basses Alpes, Valensole 1 ♀ (NMBE); Bouches-du-Rhône, St-Martin de Crau 1 ♀, 1 ♂ (MH); Gard, Nîmes 1 ♀ (ZSM); Provence, Callian 1 ♀ (NMBE); Roussillon, Argelès-sur-Mer 1 ♀, 1 ♂ (FA). ITALIEN: Abruzzi, L'Aquita, Fonte Cerreto 1 ♂ (ZSM); Aostatal, Sarre 1 ♀ (CS); Bozen 1 ♂ (NMBA), 1 ♀ (DEI), 10 ♀, 8 ♂ (NMW); Bozen, St. Pauls 23 ♀ (NMW); Lavagna 1 ♀ (ZSM); Lecco, Mte. Baro 1 ♀ (ETHZ); Lecco, Pusiano 12 ♀ (ETHZ); Sizilien, Siracusa 1 ♀ (NMBE); Triest, Conconello 2 ♀ (NMW); Vinschgau, Meran 1 ♀ (ZSM). KROATIEN: Krk, Baska 2 ♀, 2 ♂ (ZSM); Krk, Hvar 3 ♀, 3 ♂ (ZSM); Krk, Rudina 2 ♀ (ZSM). ÖSTERREICH: Burgenland, Winden 29 ♀, 5 ♂ (NMW); Kärnten, Podcetrtek 1 ♀ (ZSM); Niederösterreich, Furth 1 ♂ (NMW); Oberösterreich, Linz 1 ♂ (NMW); Salzburg, Glau-Moos am Heustadl 1 ♀, 3 ♂ (ZSM); Salzburg, Porsch 1 ♀ (ZSM); Wien, Mauer 2 ♂ (NMW). SLOWENIEN: Ljubljana [Laibach, Carniolia] 3 ♀, 1 ♂ (ZSM).

Diagnose ♀: Körper schwarz mit folgenden Teilen gelb: Scapus von dunkel bis ganz hell; Pronotum vorne mit kurzem, hinten mit langem Querband (Abb. 4a'), manchmal das Sklerit vollständig eingerahmt; Mesoscutum selten mit 2 läng-

lichen Flecken lateral; Scutellum am Hinterrand mit schmalem bis mässig breitem Querband; Metapleuron teilweise bis vollständig hell; Pro- und Mesocoxa vereinzelt mit kleinem Fleck, Metacoxa ventral oft mit variablem Apikalfleck; Pro- und Mesofemur apikal zu 1/3 bis 1/10, Metafemur meistens basal und apikal mit je einem Fleck, diese manchmal breit verbunden; Tibien und Tarsen grösstenteils: Protibia oft lateral, Metatibia immer ventral dunkel; Gastralterga 1, 4, 5 und 7 mit variabler Zeichnung (Abb. 4c'): Terga 1 und 5 mit breitem Querband, beim ersten durch die Längsfurche unterbrochen (Abb. 5b); Terga 4 und 7 mit lateralen Flecken, welche manchmal reduziert sind und auf Tergum 4 gelegentlich sogar fehlen.

Clypeus deutlich vorgezogen, lateral mit aufgebogenen Lappen, welche nach unten leicht konvergieren (Abb. 5a); Flagellum schlank, leicht keulenförmig, Glieder 2-4 quadratisch oder länger als breit; Pronotum mit 3 Querkielen: ein kurzer ungefähr in der Mitte, gefolgt von zwei längeren im hinteren Viertel respektive fast unmittelbar entlang des Hinterrandes (Abb. 4a'); Dorsellum am Hinterrand nur leicht ausgerandet, Zähne daher undeutlich; basaler Zahn des Metafemurs breit, deutlich länger als die folgende Reihe sehr kleiner Zähne (ähnlich *L. biguetina*, Abb. 2a"); Längsfurche des 1. Gastraltergums an der Basis kaum verjüngt (Abb. 5b); Längsfurche des 5. Gastraltergums oberflächlich, Ovipositorscheide in Ruhelage immer ganz sichtbar (Abb. 4c'); Ovipositorscheide 1.53-1.92 mal so lang wie der Metafemur (Abb. 12), reicht normalerweise mindestens bis zur Basis des 1. Tergums, oft bis zum Scutellum.

Körperlänge 5.7-13.2 mm (Abb. 13), Kopfbreite 1.60-3.15 mm (Abb. 14).

D i a g n o s e ♂: Gelbe Zeichnungselemente mässig bis stark reduziert, kleine Exemplare gelegentlich bis auf helle Stellen an Pronotum, Beinen und Gaster vollständig dunkel; Querbänder auf dem Gaster oft durchgehend.

Flagellum leicht gedrungener. Gaster im basalen Drittel leicht verschmälert (Abb. 2b').

Körperlänge 5.0-10.5 mm (Abb. 13), Kopfbreite 1.35-2.55 mm (Abb. 14).

V e r b r e i t u n g : Paläarktisch, östlich bis Tadschikistan (Bouček, 1974); in Mitteleuropa aus allen Ländern nachgewiesen (vgl. Bouček, 1959; Madl, 1989; Schletterer, 1890; Schmid-Egger, 1995; Schmidt, 1969; Wolf, 1953). In der Schweiz kommt die Art an wenigen Stellen im Jura, Mittelland und Graubünden und an recht zahlreich Orten in der Südschweiz (GE, VS und TI) vor (Abb. 10). Nach 1950 wurde *L. dorsigera* nur manchmal (26% der Daten, 42% der Fundpunkte auf der Verbreitungskarte) gesammelt. Die Verbreitung stimmt recht gut mit derjenigen der potentiellen Wirte überein, wobei diese zusammen ein deutlich grösseres Gebiet besiedeln (z. B. die Alpen und das Engadin) (Abb. 10).

H ö h e n v e r b r e i t u n g : von 240 bis 1125 m ü. M. (Abb. 10).

G e f ä h r d u n g : nicht gefährdet. Die meisten der potentiellen Wirte (vgl. Biologie) werden in der Roten Liste (Amiet, 1994) als nicht gefährdet aufgeführt.

B i o l o g i e : Aus Nestern von *Anthidium diadema* Latreille (Fabre, 1886), *A. strigatum* (Panzer) (Saunders, 1875 sub *A. contractum*), *Osmia adunca* (Panzer) (Amiet, pers. Beob.; Grandi, 1961; Müller *et al.*, 1997; Westrich, 1989), *O. bicornis* (Linnaeus) (Bouček, 1970; Le Goff, 1999 und Schletterer, 1890 sub *O. rufa*), *O. fedtschenkoi* (Morawitz) (Herting, 1977), *O. niveata* (Fabricius) (Herting, 1977 und Wolf, 1953 sub *O. fulviventris*) und *O. tricornis* Fabricius (Le Goff, 1999) gezogen. Ferner wurde das folgende Exemplar mit zuverlässigen Wirtsangaben untersucht:

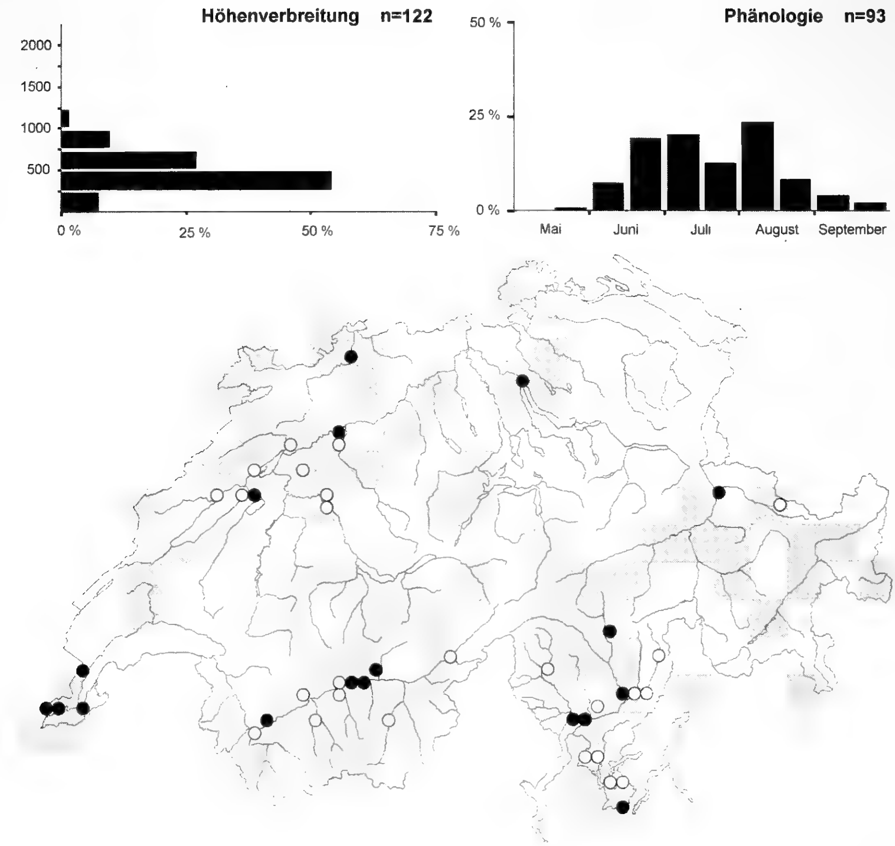


ABB. 10, *L. dorsigera*: Höhenverbreitung, Phänologie und Verbreitung in der Schweiz; ● Funde nach 1950, ○ Funde vor 1951, potentielle Wirte (Auswertung von 213 Datensätzen von *Anthidium strigatum*, *Osmia adunca*, *O. bicornis*, *O. ligurica* und *O. niveata*). Der Fundort bei Merishausen (SH) konnte auf der Verbreitungskarte nicht mehr berücksichtigt werden.

ITALIEN: Toskana, Volterra 1 ♀, 10.1985, ex Nest *Osmia ligurica* Morawitz, leg. F. Amiet (FA).

Reder (pers. Beob.) fing in seinem Garten ein Weibchen an Bruthölzern, worin seit vielen Jahren *Osmia cornuta* (Latreille), *O. parietina* Curtis, *O. bicornis* und *Megachile ericetorum* Lepeletier brüteten. Grandi (1961) beobachtete *L. dorsigera* an alten Gängen von Bostrichiden und Cerambyciden (Coleoptera), die von Bienen der Gattung *Eriades* [= *Osmia*] besiedelt waren. Die Angabe von *Bostrichus monacha* (Fabricius) (Coleoptera: Bostrichidae) in Herting (1973) ist gewiss ebenfalls auf die in den Gängen des Käfers nistende Biene zu beziehen.

Imagines erscheinen von Mai bis September (Abb. 10) und werden meist an offenen, sonnigen Standorten wie Trocken- und Halbtrockenrasen, aber auch grösseren Waldlichtungen angetroffen. Einzelne Exemplare konnten auf Blüten von *Daucus*

carota Linnaeus und anderen Doldengewächsen (Apiaceae) sowie *Euphorbia* (Euphorbiaceae) beobachtet werden (vgl. Material; Amiet, Burger, Merz, pers. Beob.; Chevrier, 1870; Pagliano, 1998). Aufgrund der zahlreich nachgewiesenen Männchen darf angenommen werden, dass sich *L. dorsigera* in der Schweiz in erster Linie bisexuell (arrhenotok) fortpflanzt.

Leucospis biguetina Jurine, 1807 2a", 4a-4c, 11-14

Untersuchtes Material: Lectotypus ♀, ohne Fundortsangabe [Herkunft nach Bouček (1974): Schweiz], coll. L. Jurine (MHNG). Schweiz: VS: ohne Fundortsangabe: 1 ♀, coll. Naumberg (DEI). Ausserberg: 1 ♀, 29.7.1933, leg. M. Naef (WL). Chandolin, Soussillon: 2 ♀, 30.6.1921, leg./coll. T. Steck (NMBA). Euseigne: 1 ♀, 14.8.1933, leg. M. Naef (WL). Grengiols: 1 ♀, 22.6.1998, leg./coll. F. Amiet (NMBE). Grimentz: 1 ♀, 17.7.1978, leg./coll. F. Amiet (NMBE). Hérémence: 1 ♀, 23.7.1992, leg. F. Amiet (FA). Hohtenn: 2 ♀, 10.8.1930, 2 ♀, 21.8.1932, 1 ♀, 29.7.1934, 2 ♀, 7.7.1935, leg. M. Naef (WL); 1 ♀, 29.7.1987, leg. F. Amiet (FA); 1 ♀, 29.7.1987, leg./coll. F. Amiet (NMBE). Hohtenn, Ladu: 1 ♀, 15.7.1991, leg. F. Amiet (FA). Lens: 1 ♀, 11.7.1967, 1 ♀, 13.7.1967, 4 ♀, 16.7.1967, an Apiaceae (MHNG); 1 ♀, 22.7.1927, leg. T. Steck (NMBE). Martisberg: 1 ♀, 21.7.1992, leg./coll. F. Amiet (NMBE). Niedergesteln: 1 ♀, 8.8.1998, leg. F. Amiet (FA). Niouc: 2 ♀, 12.7.1908, leg. T. Steck (NMBE). Pfynwald: 1 ♀, 29.6.1924, leg./coll. T. Steck (NMBA); 1 ♀, 18.7.1958, 1 ♀, 2.8.1960, leg. Daicker (MHNG); 1 ♀, 7.1958, 1 ♀, 10.7.1975, leg./coll. F. Amiet (NMSO); 1 ♀, 10.7.1975, 2 ♀, 17.7.1975, 1 ♀, 8.7.1979, leg. F. Amiet (FA); 1 ♀, 10.7.1976, leg./coll. F. Amiet (NMBE); 1 ♀, 6.7.1997, leg. B. Merz (NMBE); 1 ♀, 12.8.1997, leg. B. Merz (ETHZ). Sierre: 2 ♀, coll. A. von Schulthess (ETHZ); 1 ♀, leg./coll. O. Schmiedeknecht (DEI); 2 ♀, leg. O. Schmiedeknecht (NMW); 1 ♀, leg./coll. O. Schmiedeknecht (MNHU); 1 ♀, leg./coll. O. Schmiedeknecht (ETHZ); 1 ♀, leg./coll. T. Steck (NMBA); 1 ♀ (DEI); 1 ♀ (MHNG); 1 ♀, 12.7.[?18...] (MHNG); 1 ♀, 15.7.1884, leg. H. Friese, coll. A. von Schulthess (ETHZ); 1 ♀, 6.9.1887, leg. M. Paul, coll. A. von Schulthess (ETHZ); 1 ♀, 18.7.1900, 1 ♀, 29.6.1901, 3 ♀, 30.6.1901, leg./coll. E. Frey-Gessner (MHNG); 3 ♀, 26.6.1901, coll. A. von Schulthess (ETHZ); 2 ♀, 5.7.1908, leg. T. Steck (NMBE). Simplon, Berisal: 1 ♀, 29.7.1939, leg./coll. A. Nadig (ETHZ). Sion: 1 ♀, 30.7.1892, leg./coll. T. Steck (NMBA); 1 ♀, 30.8.1892, leg. T. Steck (NMBE). Sion, Château de la Soie: 2 ♀, 9.7.1968, an *Euphorbia* (MHNG); 1 ♀, 13.7.1968, an *Euphorbia* (MHNG). St. German: 1 ♀, 23.7.1970, leg./coll. F. Amiet (NMBE). St. Niklaus: 1 ♀, 15.7.1925, leg./coll. E. Däniker (NMBE). Stalden: 1 ♀, 30.7.1924, leg./coll. T. Steck (NMBA); 2 ♀, 9.8.1933, leg. M. Naef (WL); 1 ♀, 7.7.1997, leg. G. Carron (GC [nicht untersucht]). Visp-Stalden: 1 ♀, 31.7.1932, 1 ♀, 8.8.1933, 1 ♀, 21.7.1935, leg. M. Naef (WL). Zeneggen: 1 ♀, 14.7.1970, 1 ♀, 23.7.1972, 1 ♀, 8.7.1973, leg. F. Amiet (FA); 1 ♀, 22.7.1986, leg./coll. F. Amiet (NMBE).

FRANKREICH: Ariège, Verdun 1 ♂ (SMNS); Korsika, Vizzavona 1 ♀ (MHNG). GRIECHENLAND: Hellas, Oros Killini, Ano Trikala 1 ♀ (WA). ITALIEN: Postumia 1 ♀ (DEI); Sizilien, Taormina 2 ♂ (ETHZ), 3 ♀, 2 ♂ (ZSM); Vinschgau, Kastelbell 1 ♂ (ES); Vinschgau, Latsch 1 ♂ (ES); Vinschgau, Malserheide 1 ♂ (ETHZ); Vinschgau, Schluderns 3 ♀, 3 ♂ (BZOL). KROATIEN: Krk, Baska 1 ♀ (ZSM). ÖSTERREICH: Burgenland, Piesting 1 ♀ (NMW); Burgenland, Winden 10 ♀ (NMW); Wien, Donau-Au 1 ♀ (BZOL). SLOWENIEN: Istrien, Portorož [Pirano] 1 ♂ (ZSM). SPANIEN: Leon, Ponferrada 1 ♀ (CS). TÜRKEI: Kayseri, Göreme 1 ♀ (CS); Taurus, Marasch 1 ♀ (ZSM).

Diagnose ♀ ähnlich der von *L. dorsigera*, aber: Gelbe Zeichnung an den Beinen meist leicht rötlich verfärbt; Pronotum vorne mit langem, hinten mit kurzem Querband (Abb. 4a); Mesoscutum meist mit zwei Flecken im zentralen Bereich, durchwegs mit zwei länglichen Flecken lateral (ähnlich *L. gigas*, Abb. 3d); Scutellum am Hinterrand mit in der Mitte stark eingeschnürtem Querband; Metacoxa höchstens ventro-lateral mit kleinem undeutlichen Apikalfleck; Femora apikal zu 1/2 bis 1/4

hell, Metafemur manchmal basal mit zusätzlichem Fleck (Abb. 2a"); Tibien und Tarsen hell, nur die beiden ventralen Kiele der Metatibia proximal dunkel; Gastralterga 1, 4, 5 und 7 mit variablen Querbändern (Abb. 4c), auf den Terga 1 und 4 durchgehend, auf den beiden hinteren Terga in der Mitte unterbrochen; erstes Querband in der Mitte stark eingeschnürt (Abb. 4b).

Clypeus kaum vorgezogen und mehr oder weniger verrundet (ähnlich *L. bifasciata*, Abb. 5a'); Flagellum stärker keulenförmig, Glieder 2-4 wenig kürzer als breit oder quadratisch; Pronotum mit 2 Querkielen: einer im hinteren Viertel, der andere fast unmittelbar entlang des Hinterrandes (Abb. 4a); Dorsellum stärker ausgerandet, mit 2 deutlichen Zähnen am Hinterrand; Gastraltergum 1 ohne Längsfurche (Abb. 4b), diejenige des 5. Tergums tief, so dass Ovipositorscheide in Ruhelage teilweise verdeckt ist (Abb. 4c); Ovipositorscheide kürzer, 1.02-1.23 mal so lang wie der Metafemur (Abb. 12), reicht bis zum basalen Fünftel des 5. Tergums.

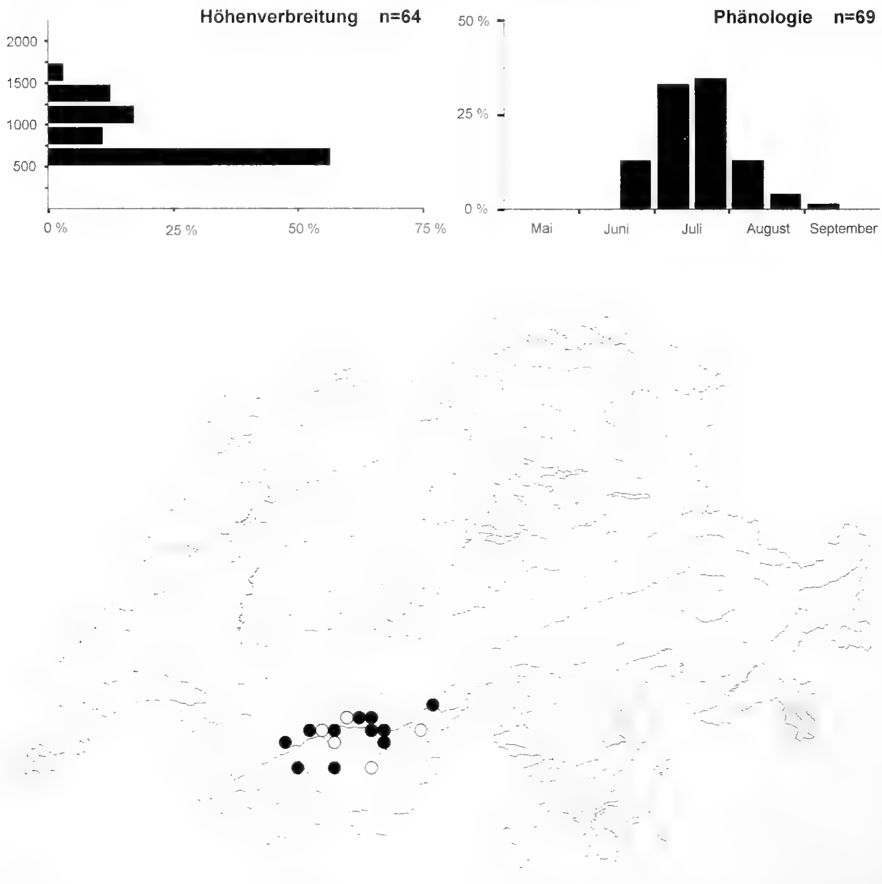


ABB. 11. *L. biguetina*: Höhenverbreitung, Phänologie und Verbreitung in der Schweiz; ● Funde nach 1950, ○ Funde vor 1951, potentielle Wirte (Auswertung von 15 Datensätzen von *Osmia acuticornis* und *O. tridentata*).

Körperlänge 5.3-11.3 mm (Abb. 13), Kopfbreite 2.05-2.60 mm (Abb. 14).

Diagnose ♂: Gelbe Zeichnungselemente gelegentlich reduziert; Querbänder auf dem Gaster meist durchgehend, Querband auf 1. Tergum nicht eingeschnürt.

Form des Gasters ähnlich *L. dorsigera* (Abb. 2b').

Körperlänge 7.0-9.2 mm (Abb. 13), Kopfbreite 2.10-2.40 mm (Abb. 14).

Verbreitung: Paläarktisch, östlich bis Tadschikistan (Bouček, 1974); in Mitteleuropa bisher nur aus der Schweiz (z. B. Schletterer, 1890; Madl, 1990), Tschechien, Slovakei (Bouček, 1959) und Österreich (Madl, 1989) nachgewiesen. In der Schweiz ist das Vorkommen auf das Wallis beschränkt (Abb. 11), wo *L. biguetina* oft auch nach 1950 (57% der Daten, 69% der Fundpunkte auf der Verbreitungskarte) gesammelt wurde. Bemerkenswert ist das Fehlen von Daten aus dem unteren Teil des Wallis, d. h. unterhalb von Sion. Die Verbreitung stimmt recht gut mit derjenigen der potentiellen Wirte überein, wobei diese in der Schweiz weiter verbreitet sind (Nordschweiz, GE, GR, TI) (Abb. 11).

Höhenverbreitung: von 500 bis 1600 m ü. M. (Abb. 11).

Gefährdung: gefährdet. Die beiden potentiellen Wirte (siehe unten) werden in der Roten Liste (Amiet, 1994) für die Südschweiz als gefährdet aufgeführt.

Biologie: Aus Nestern von *Osmia acuticornis* Dufour & Perris (Le Goff, 1996, 1997b sub *Hoplitis*) und *O. tridentata* Dufour & Perris (Le Goff, 1997a, 1997b sub *Hoplitis*) in Frankreich gezogen.

Imagines erscheinen von Juni bis September (Abb. 11) und werden normalerweise an xerothermen Standorten wie Steppen- und Trockenrasen angetroffen. Einzelne Exemplare konnten auf Blüten von Doldengewächsen (Apiaceae) und *Euphorbia* (Euphorbiaceae) beobachtet werden (vgl. Material; Amiet, Merz, pers. Beob.). Nach Bouček (1974) vermehrt sich *L. biguetina* in Mitteleuropa parthenogenetisch, wobei aus unbefruchteten Eizellen fast durchwegs Weibchen entstehen (Thelytokie). Dies trifft wahrscheinlich auch auf die Population im Wallis zu, da im reichen Untersuchungsmaterial von insgesamt 69 Exemplaren kein einziges Männchen vorhanden war. Allerdings scheint es sich hier um ein lokales Phänomen zu handeln, denn aus anderen, nahegelegenen Gebieten, z. B. dem Vinschgau im Südtirol, befanden sich unter insgesamt 9 Belegexemplaren 6 Männchen (vgl. Material).

Leucospis bifasciata Klug, 1814 — 5a', 5b', 12-14

Untersuchtes Material: ASERBEIDSCHAN: Lenikoran, Azfilial Girkan Reserve 1 ♂ (MH); NW Baku, Varafta Mts. 1 ♂ (MH). «ASIA MINOR: Namzur» 1 ♀ (ZSM). BULGARIEN: Slancev Briag 1 ♀ (BZOL); SW Melnik 1 ♂ (BZOL). FRANKREICH: Basses-Alpes, Valensole 1 ♀ (FA), 2 ♀ (NMBE). GRIECHENLAND: Kozani, Siatista, Brücke 1 ♀ (BZOL); Peloponnes, Zacharo 1 ♀(ZSM); Preveza SB, 2 km S Kerasona 2 ♂ (BZOL). ISRAEL: Antipatris 1 ♀ (ETHZ). JORDANIEN: N Shuna 1 ♂ (BZOL); Safi, 50 km of Karak 1 ♂ (BZOL). ?LIBANON: «Sarepta» 1 ♀(MHNG). SYRIEN: 20 km NE Latakia 1 ♀ (BZOL). TÜRKEI: Sultan Daglari, Yalvat 1 ♀ (BZOL). TURKMENIEN: 15 km N Aschapat 1 ♀, 1 ♂ (BZOL); Kopet-Dag Kizi-Arvat, 50 km S Chajagaia 1 ♀ (BZOL). USBEKISTAN: Yangikichlak, 10 km NW Ddjiak 1 ♂ (BZOL).

Diagnose ♀ ähnlich der von *L. dorsigera*, aber: Scutellum am Hinterrand mit in der Mitte leicht eingeschnürtem Querband, dieses oft die Mitte des Scutellums überschreitend; Querband auf Gastraltergum 5 in der Mitte unterbrochen.

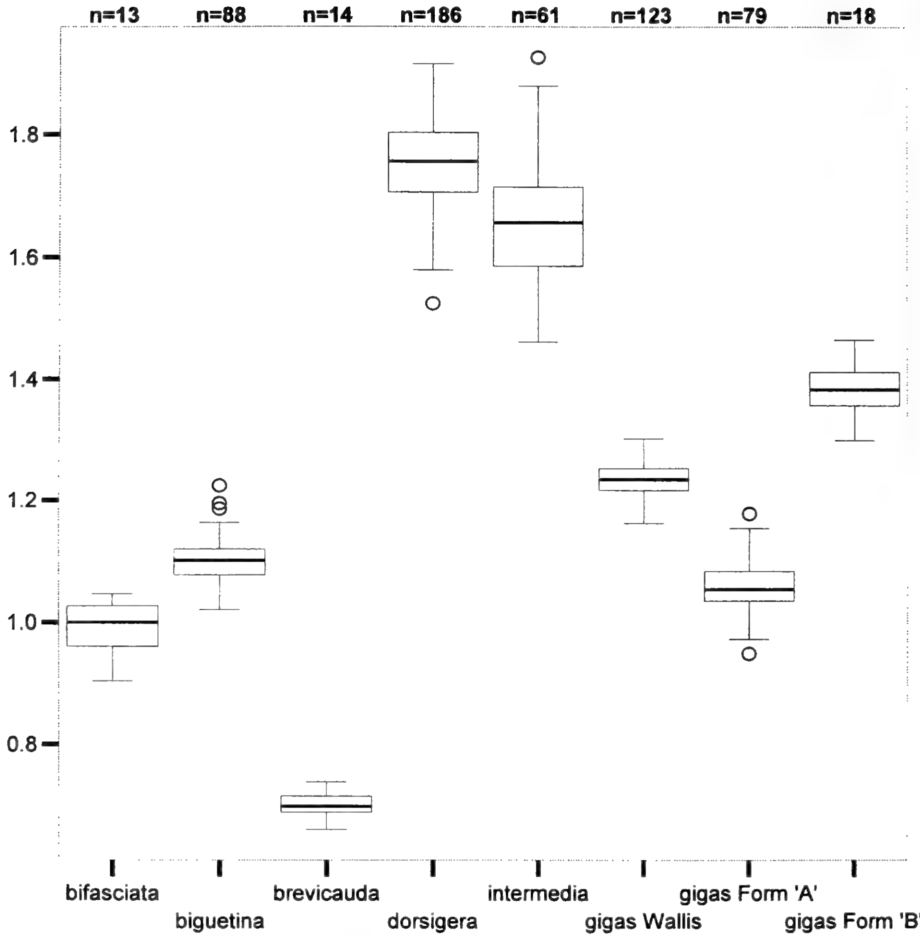


ABB. 12. Boxplot (nach Tukey) von *Leucospis*: Verhältnis Ovipositorscheide- zu Metafemurlänge. Die Grafik zeigt Median, Interquartilbreite, Variationsbreite (ohne Ausreisser), Ausreisser (○), Extremwerte (★).

Clypeus kaum vorgezogen und mehr oder weniger verrundet (Abb. 5a'); Flagellum stärker keulenförmig, Glieder 2-4 wenig kürzer als breit oder quadratisch; die beiden vorderen Querkiele des Pronotums kräftiger entwickelt als der hintere Kiel; Längsfurche des 1. Gastraltergums an der Basis deutlich verjüngt (Abb. 5b'); Ovipositorscheide kürzer, 0.90-1.05 mal so lang wie der Metafemur (Abb. 12), reicht höchstens bis zur Mitte des 1. Tergums.

Körperlänge 6.3-9.0 mm (Abb. 13), Kopfbreite 1.85-2.60 mm (Abb. 14).

D i a g n o s e ♂: Gelbe Zeichnungselemente gelegentlich reduziert; Querbänder auf dem Gaster normalerweise durchgehend.

Form des Gasters ähnlich *L. dorsigera* (Abb. 2b').

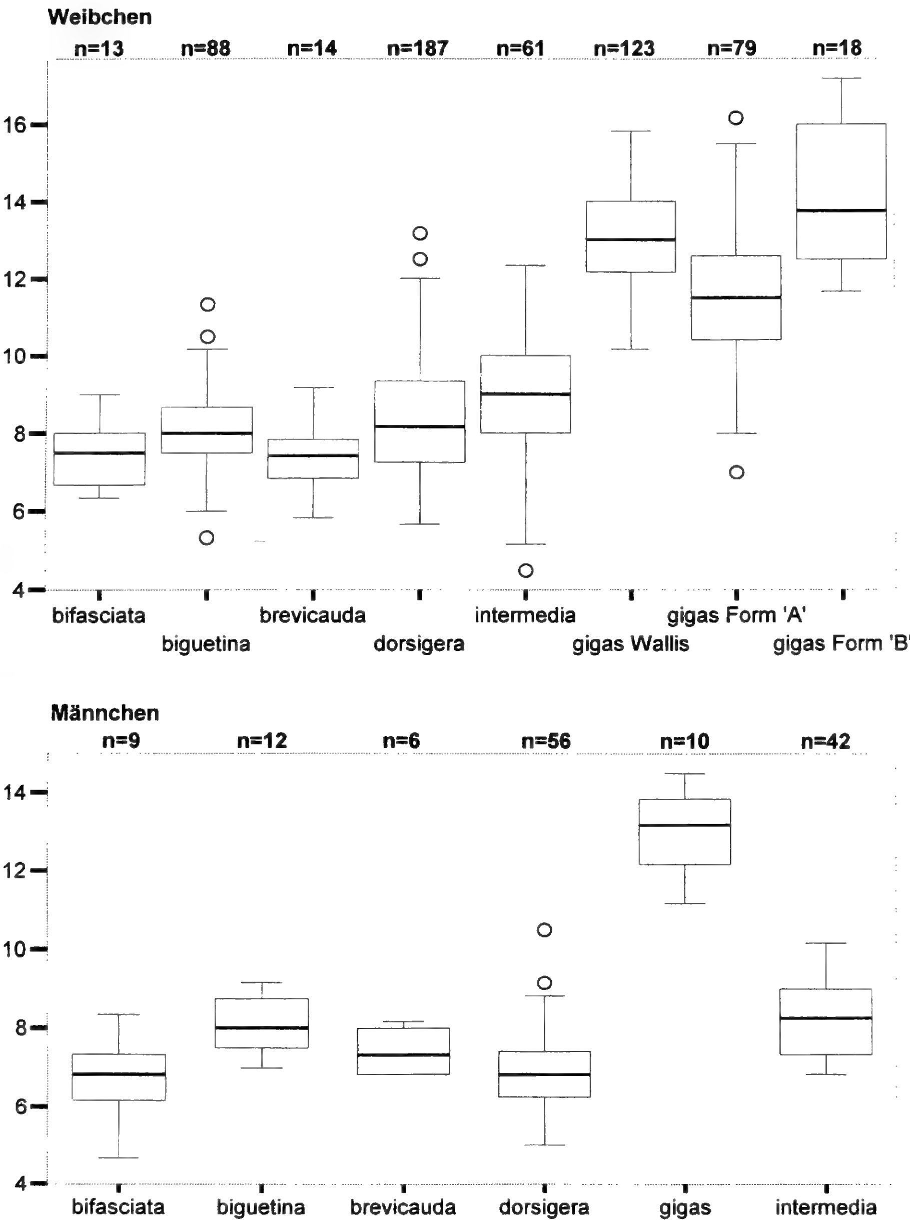


ABB. 13, Boxplot von *Leucospis*: Körperlänge in mm.

Körperlänge 4.7-8.3 mm (Abb. 13), Kopfbreite 1.40-2.30 mm (Abb. 14).
Verbreitung: Paläarktisch, östlich bis Tadschikistan (Bouček, 1974); in Mitteleuropa wurde *L. bifasciata* bisher noch nicht nachgewiesen. Der Schweiz am nächsten

gelegene Vorkommen: Frankreich, Basses Alpes, Valensole (FA, NMBE); Italien, Piemont, Oulx und Veneto, Venedig (Bouček, 1974).

B i o l o g i e : Aus Nest von *Anthidium strigatum* (Panzer) in Kroatien gezogen (Fahringer, 1922); Bestimmung des Parasitoiden überprüft von Bouček (1974).

Leucospis brevicauda Fabricius, 1804 2a-b, 12-14.

Untersuchtes Material: ALGERIEN: El Afroun 1 ♂ (MHNG). ITALIEN: Puglia, Mt. Gargano, Cagnavo 1 ♀ (BZOL); Sardinien, Siniscola 1 ♀ (FNSM). MAROKKO: 4 ♀ (MHNG); 70 km N Agadir, Tamri 1 ♀ (BZOL); 100 km E Bouzakame, Icht 1 ♂ (BZOL); Tanger 4 ♀, 3 ♂ (MHNG); 10 km S Taroudant 1 ♂ (BZOL). TUNESIEN: Gabès, Skhira 2 ♀ (MH); Gafsa-El Guetar 1 ♀ (BZOL); Metouia 1 ♂ (MH).

D i a g n o s e ♀ ähnlich der von *L. dorsigera*, aber: Flagellum rötlich; Zeichnung neben schwarz und gelb auch rotbraun; gelbe Zeichnung häufig stärker ausgedehnt als bei *L. dorsigera*, besonders an Pronotum, Mesoscutum, Scutellum und Gaster; Metafemur ausser an den Zähnen und an der Basis gelb (Abb. 2a); Metatibia dorsal rotbraun bis schwarz, höchstens in der Mitte mit feinem gelblichem Längsstreifen; Tarsen meist rotbraun; Gastralterga 1, 4, 5 und 7 mit variablen Querbändern, auf den Terga 1 und 4 manchmal, auf Terga 5 und 7 immer in der Mitte unterbrochen; 5. Tergum meist zusätzlich mit kleinen Flecken; auf dem 7. Tergum helle Zeichnung rotbraun, daher oft undeutlich.

Clypeus kaum vorgezogen und mehr oder weniger verrundet (ähnlich *L. bifasciata*, Abb. 5a'); die beiden vorderen Querkiele des Pronotums kräftiger entwickelt als der hintere Kiel; basaler Zahn des Metafemurs ungefähr so lang wie folgende Zähne (Abb. 2a); Gastralterga 1-4 ohne Längsfurche (ähnlich *L. biguetina*, Abb. 4b), diejenige des 5. Tergums tief, so dass Ovipositorscheide in Ruhelage teilweise verdeckt ist (ähnlich L. biguetina, Abb. 4c); Ovipositorscheide sehr kurz, 0.66-0.74 mal so lang wie der Metafemur (Abb. 12), reicht nur bis zur Mitte oder zum basalen Drittel des 5. Tergums.

Körperlänge 5.8-9.2 mm (Abb. 13), Kopfbreite 1.90-2.45 mm (Abb. 14).

D i a g n o s e ♂: Gelbe Zeichnungselemente gelegentlich reduziert; Querbänder auf dem Gaster durchgehend.

Gaster im basalen Drittel stark verschmälert (Abb. 2b).

Körperlänge 6.8-8.2 mm (Abb. 13), Kopfbreite 1.45-2.15 mm (Abb. 14).

V e r b r e i t u n g : Circum-mediterran (Bou„ek, 1974); in Mitteleuropa wurde *L. brevicauda* bisher noch nicht nachgewiesen. Der Schweiz am nächsten gelegene Vorkommen: Frankreich, Hérault, Palavas (Berland, 1934b) und Bouches-du-Rhône, Port du Bouc (Bouček, 1974); Italien, Puglia, Mt. Gargano (BZOL).

B i o l o g i e : Wirt unbekannt.

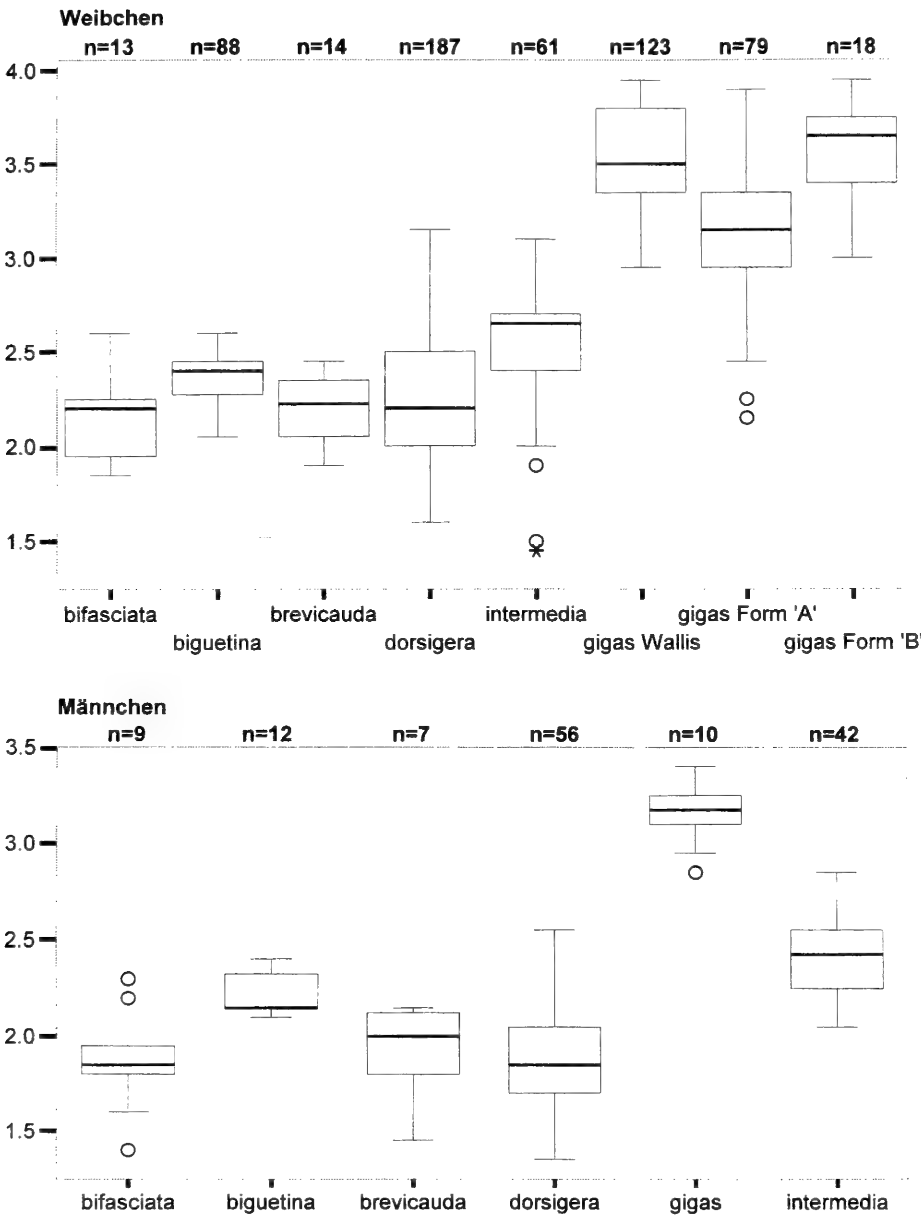


ABB. 14, Boxplot von *Leucospis*: Kopfbreite in mm.

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The *Bufo tuberosus* species group with the description of a new species from the rainforest of Côte-d'Ivoire

Mills TANDY[1] & Jean-Luc PERRET[2]
[1] Colorado State University
201 Highland Drive
Sierra Vista, Arizona 85635 USA.
[2] Département d'herpétologie et d'ichtyologie
Muséum d'histoire naturelle
Route de Malagnou 1, case postale 6434
CH-1211 Genève 6, Suisse.

The *Bufo tuberosus* species group with the description of a new species from the rainforest of Côte-d'Ivoire. - A very small species of toad similar to *Bufo tuberosus* was discovered in a collection made in West Africa by M. Lamotte in the late 1960s. In the 1980s a second specimen of this species from Côte-d'Ivoire was donated to the Muséum d'histoire naturelle de Genève. This paper describes the new species, *B. amieti*, presents additional data on *B. tuberosus*, compares these species to others and hypothesizes an origin of *B. amieti* and *B. tuberosus* by geographical isolation of a common ancestor in eastern and western blocks of equatorial rainforest separated by the V-Baoulé during past interpluvial periods.

Key-words: *Bufo* - *Bufo tuberosus* group - speciation - Côte-d'Ivoire - rain forest - West Africa - Anura.

INTRODUCTION

This paper summarizes the biology of the central African rainforest toad *Bufo tuberosus* Günther and describes a new species of the same group from the far western section of African equatorial lowland rainforest in Côte-d'Ivoire.

Bufo tuberosus, a very distinctive species from the rainforests of central Africa, was described in the mid nineteenth century. It is so morphologically different from other African *Bufo* with its usually globose parotoid glands and extreme development of spinose warts that it was placed in its own species group (Tandy, 1972; Tandy & Keith, 1972). Although *Bufo tuberosus* was described very early in the literature on African amphibians, and collections have been made by various investigators over the years, it is not a common amphibian in museum holdings. Little is known about its behavior and nothing about its genetics. This paper analyzes

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morphological variation based on museum material, reports observations of its calling behavior and recordings of its mating call made in Camerounian rainforests by Amiet (1973, 1975, 1976, 1989) and by Tandy & Tandy (1976) and considers ecological features of known localities.

In the 1970's, Tandy encountered a small toad in a collection from Grabazouo, Côte-d'Ivoire made by M. Lamotte and R. Vuatroux. This is a gravid female that resembles *Bufo tuberosus* but which is half the size of adult females of that species. In 1986, J.-L. Perret received a second female of this species, collected by R. Neumeyer, from Taï, Côte-d'Ivoire. This paper describes these specimens as a new species and compares them to *Bufo tuberosus* and other species from central and western Africa. The new species is named in honor of our colleague who has contributed so much to central African herpetology, J.-L. Amiet.

Terminology and methods of data collection and analysis are given in Tandy (1972), Tandy & Keith (1972), Tandy & Tandy (1976), Largen *et al.* (1978), Tandy *et al.* (1982), Tandy *et al.* (1985) and Tandy & Feener (1985).

Data are presented in the following format: locality, geographic coordinates; sex and collection numbers of specimens; collection numbers of tape recordings; altitude; date of collection; collector.

The following abbreviations are used for collection numbers:

AMNH	American Museum of Natural History, New-York;
BM	British Museum (Natural History), London;
CAS	California Academy of Sciences, San Francisco;
CNHM	Chicago Natural History Museum, Chicago;
FM	Field Museum of Natural History, Chicago;
MBG	Mission Biologique au Gabon;
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts;
MHNB	Muséum d'histoire naturelle, Bâle;
MHNG	Muséum d'histoire naturelle, Genève;
MHNCF	Muséum d'histoire naturelle, La Chaux-de-Fonds;
MNHP	Muséum national d'histoire naturelle, Paris;
MT	Collection of M. Tandy;
MT()	Reference number of M. Tandy assigned to specimen of collection indicated within parentheses;
MT.TC.Ca	Collection of tape recordings of M. Tandy; tape cut from Cameroun;
RGMC	Registre général du Musée du Congo, Tervuren;
SMF	Natur-Museum und Forschungsintitut Senckenberg, Frankfurt;
UMMZ	Museum of Vertebrate Zoology, University of Michigan, Ann Arbor, Michigan;
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn;
ZMB	Zoologisches Museum der Humboldt Universität, Berlin.

Bufo amieti sp. n.

Holotype: 1 adult female (MHNG 2594.17) from lowland rainforest near Taï, Taï National Park, Côte-d'Ivoire (5° 52'N 7°28'W, altitude 123m) collected in 1986 by R. Neumeyer.

FIG. 1. *Bufo amieti* sp. n. Holotype female (above): habitus, natural size; (below): detail of the enormous paratoid gland, tympanum and eye.

Paratype: 1 adult female (MNHP 1997 4934 = MT(P) 6141) from lowland rainforest on the Sassandra River near Grabazouo, Soubré, Côte-d'Ivoire (5° 50'N 6° 35'W, altitude ~150m) collected 10.XII.1967 by M. Lamotte and R. Vuatroux.

Diagnosis

A very small species of *Bufo* resembling *Bufo tuberosus* Günther, 1858, but only half the size of that species. Body measurements and their ratios indicate at least five diagnostic differences with all species to which *B. amieti* has been compared

FIG. 2. *Bufo amieti* sp. n. Holotype female: dorsal and ventral color pattern. Magnification 2X.

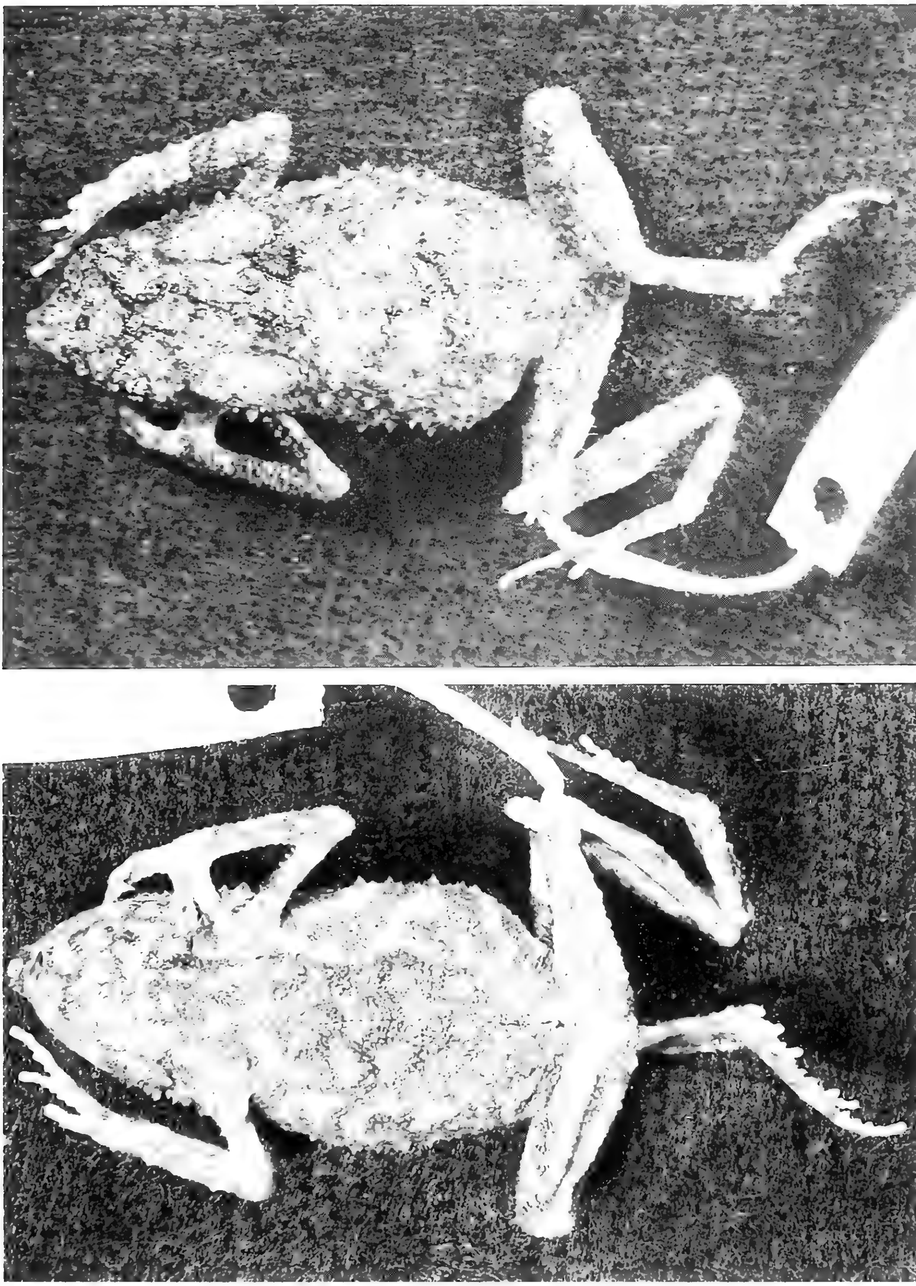

FIG. 3. *Bufo amieti* sp. n. Paratype female: dorsal and ventral color pattern. Magnification 2X.

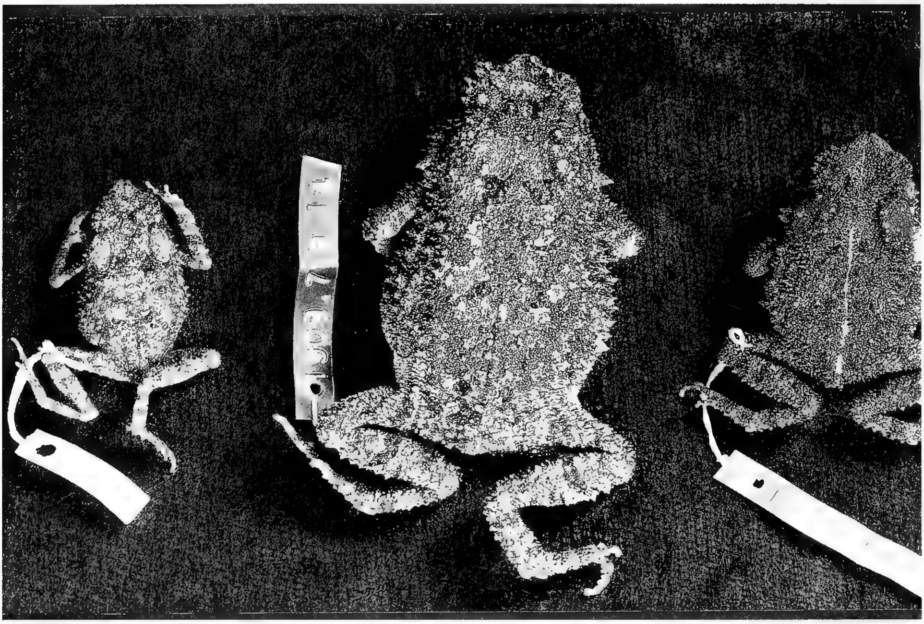

FIG. 4. *Bufo amieti* sp. n. female (paratype: MHNP 1997 4934); snout-urostyle length 35.9 mm. Grabazouo, Soubré. Côte d'Ivoire; *Bufo tuberosus* female (BM 1909.7.9.14); SU 65.8 mm. Efangono, Cameroun; B. tuberosus male (BM 1934.12.1.14); SU 45.0 mm. Lomié District, Cameroun.

(Tables 1 - 3). Comparisons have been made with all species of *Bufo* known from the geographic area concerned, west and central Africa, and with all members of the *Bufo regularis* Complex because of the acoustical similarities between the mating call of *Bufo tuberosus* and species of that complex. The ratio of tympanum diameter/parotoid width separates *B. amieti* from almost all congeners. Tympanum diameter, snout-urostyle length or parotoid length/parotoid width distinguish it from the others. Tympanum distinct, its horizontal diameter approximately 0.12 the width of the head and 0.18 the width of the parotoid; snout-urostyle length about 37mm; parotoid length 1.7 times the parotoid width; no tarsal fold; male unknown; first finger longer than second; toes not extensively webbed ($3^3/_4$ phalanges of fourth toe free of webbing on both inner and outer margins); lacking series of warts on posterior surface of forearm; large warts with multiple cornified spinules extensively developed. Ecological data for two localities: lowland rain forest, altitude,

$\bar{x}$ = 136.5m, range (123-150); mean annual rainfall, $\bar{x}$ = 173.70cm (161.1-186.3); mean annual temperature, $\bar{x}$ = 23.95°C (23.9-24)(Table 4).

DESCRIPTION

Holotype: Snout-urostyle length (SU) 37.7mm; form moderately stout; head triangular, broader than long, head width (HW) 15.5mm, head length (HL) 10.2mm; snout obtusely rounded; nostrils closer to tip of snout than to eye; canthus rostralis

TABLE 1. Linear measurements and their ratios for *Bufo amieti* and other species from west and central Africa. SU = snout-urostyle length, HW = head width, HL = head length, T = horizontal diameter of the tympanum, E = horizontal diameter of the eye, PL = parotoid length, PW = parotoid width, UH = urostyle-heel length. All measurements are in mm.

	n	Snout-urostyle	Head width	Head length	Tympanum diameter	Eye diameter	Paratoid length	Paratoid width	Urostyle-heel	SU/HW	HW/HL	T/HW	PL/PW	HW/PL	T/PL	HW/PW	T/PW	SU/UH
Bufo amieti																		
Côte d'Ivoire																		
Grabazouo		35.9	12.4	8.0	1.5	3.4	7.3	3.9	25.6	2.90	1.55	0.12	1.87	1.70	0.21	3.18	0.17	1.40
Taï		37.7	15.5	10.2	1.8	4.1	9.6	6.0	26.5	2.43	1.52	0.12	1.60	1.61	0.19	2.58	0.20	1.42
Mean - females	2	36.8	13.95	9.1	1.65	3.75	8.45	4.95	26.05	2.664	1.535	0.119	1.736	1.657	0.196	2.881	0.183	1.412
Minimum		35.9	12.4	8	1.5	3.4	7.3	3.9	25.6	2.43	1.52	0.12	1.60	1.61	0.19	2.58	0.17	1.40
Maximum		37.7	15.5	10.2	1.8	4.1	9.6	6	26.5	2.90	1.55	0.12	1.87	1.70	0.21	3.18	0.20	1.42
Bufo tuberosus																		
Cameroun, Guinea Ecuatorial, République Démocratique du Congo																		
Mean - females	31	63.11	22.84	13.57	3.19	6.74	11.58	7.17	50.98	2.769	1.705	0.139	1.636	1.997	0.277	3.239	0.354	1.244
Standard Error		0.833	0.323	0.294	0.091	0.136	0.260	0.195	0.928	0.0294	0.0418	0.0032	0.0395	0.0460	0.0076	0.0788	0.0101	0.0152
Minimum		54.3	19.3	11.3	2.4	4.5	9.3	5.4	41.9	2.50	1.30	0.11	1.07	1.44	0.22	2.38	0.27	1.11
Maximum		71.4	26.6	17.5	4.0	8.2	15.1	9.5	63.6	3.22	2.12	0.18	2.03	2.45	0.36	4.07	0.44	1.43
Cameroun, Guinea Ecuatorial																		
Mean - males	11	39.20	15.63	9.39	2.28	4.95	7.77	4.95	33.09	2.513	1.677	0.145	1.583	2.032	0.294	3.203	0.253	1.188
Standard Error		1.431	0.608	0.436	0.141	0.271	0.355	0.223	1.165	0.039	0.046	0.007	0.060	0.071	0.014	0.151	0.016	0.021
Minimum		32.8	13.4	7.2	1.6	3.8	6.4	3.5	28.4	2.33	1.46	0.11	1.33	1.75	0.21	2.70	0.18	1.08
Maximum		48.1	20.1	12.0	3.0	6.2	10.0	6.2	39.7	2.80	1.90	0.18	1.94	2.38	0.37	4.57	0.33	1.33
Bufo gracilipes																		
Cameroun, Gabon																		
Mean - females	11	34.58	12.35	8.32	2.26	3.67	6.96	2.40	27.60	2.802	1.497	0.184	3.186	1.827	0.336	5.666	0.252	1.256
Standard Error		0.590	0.223	0.261	0.036	0.118	0.339	0.194	0.593	0.0401	0.0437	0.0038	0.3995	0.1136	0.0249	0.6715	0.0040	0.0211
Minimum		31.4	11.1	6.5	2.1	3.1	4.0	1.1	24.4	2.62	1.27	0.16	1.54	1.49	0.28	3.68	0.23	1.14
Maximum		37.8	13.6	9.6	2.5	4.6	8.1	3.4	30.3	3.02	1.77	0.20	6.55	2.88	0.58	11.09	0.28	1.37
Mean - males	11	28.39	10.34	7.34	1.84	3.18	5.71	2.34	22.56	2.752	1.416	0.180	2.604	1.862	0.334	4.622	0.204	1.257
Standard Error		1.036	0.397	0.295	0.078	0.163	0.357	0.206	0.710	0.0370	0.0435	0.0095	0.2823	0.1067	0.0232	0.3055	0.0086	0.0125
Minimum		23.8	8.6	6.3	1.5	2.4	4.1	1.6	19.9	2.51	1.25	0.13	1.78	1.46	0.20	3.14	0.17	1.20
Maximum		36.8	13.2	9.7	2.2	4.4	7.6	4.2	28.1	2.97	1.65	0.24	4.63	2.33	0.42	6.75	0.24	1.33

	n	Snout urostyle	Head width	Head length	Tympanum diameter	Eye diameter	Paratoid length	Paratoid width	Urostyle-heel	SU/HW	HW/HL	T/HW	PL/PW	HW/PL	T/PL	HW/PW	T/PW	SU/UH
Bufo villiersi Cameroun																		
Mean - females	7	63.97	22.83	12.44	3.27	6.04	13.93	6.16	49.90	2.806	1.842	0.142	2.284	1.653	0.236	3.727	0.363	1.287
Minimum		52.3	19.1	10.5	1.9	5.3	12.5	4.9	38.4	2.56	1.71	0.10	1.92	1.49	0.15	3.24	0.21	1.20
Maximum		69.0	26.0	15.0	4.0	7.0	15.2	7.2	56.1	3.07	2.09	0.16	2.62	2.08	0.32	4.00	0.44	1.36
Mean - males	6	54.85	19.28	11.92	2.80	5.90	12.00	4.90	44.87	2.849	1.625	0.146	2.452	1.613	0.235	3.957	0.311	1.234
Minimum		54.0	18.0	10.8	2.0	5.1	11.2	4.5	41.0	2.68	1.52	0.10	2.30	1.46	0.17	3.45	0.22	1.00
Maximum		56.5	20.5	13.5	3.5	6.5	13.0	5.5	55.0	3.06	1.80	0.18	2.60	1.78	0.31	4.56	0.39	1.34
Bufo danielae Monogaga, Côte d'Ivoire																		
Mean - females	3	44.6	16.4	11.1	2.4	5.4	11.3	5.0	32.9	2.723	1.480	0.144	2.241	1.462	0.211	3.266	0.473	1.356
Minimum		42.9	15.6	9.9	2.1	5.2	10.3	4.8	30.6	2.70	1.32	0.13	2.13	1.36	0.18	2.89	0.39	1.31
Maximum		46.8	17.2	11.8	2.5	5.6	12.0	5.4	34.4	2.75	1.65	0.15	2.45	1.67	0.24	3.58	0.52	1.40
Mean - males	22	37.78	13.68	9.94	2.18	4.77	8.04	3.63	29.23	2.765	1.379	0.159	2.220	1.729	0.276	3.784	0.603	1.293
Standard Error		0.593	0.239	0.176	0.048	0.081	0.263	0.083	0.372	0.0155	0.0183	0.0027	0.0634	0.0474	0.0089	0.0616	0.0141	0.0127
Minimum		32.0	11.5	8.6	1.7	4.1	5.9	3.0	26.1	2.66	1.20	0.13	1.73	1.31	0.19	3.31	0.48	1.21
Maximum		44.4	16.5	11.5	2.6	5.9	10.7	4.6	33.7	2.92	1.57	0.19	2.86	2.14	0.36	4.48	0.72	1.45
Bufo camerunensis Cameroun, Nigeria, République du Congo																		
Mean - females	13	66.89	27.08	15.81	4.72	7.11	14.67	5.25	54.83	2.472	1.729	0.174	2.890	1.866	0.324	5.372	0.934	1.236
Standard Error		1.311	0.526	0.529	0.136	0.187	0.487	0.336	1.089	0.0263	0.0482	0.0034	0.1451	0.0627	0.0116	0.2915	0.0542	0.0163
Minimum		58.3	24.0	12.8	3.4	6.2	12.8	3.5	48.2	2.31	1.52	0.14	2.03	1.49	0.26	3.51	0.60	1.18
Maximum		74.1	30.1	18.4	5.4	8.4	18.4	7.8	63.0	2.61	2.02	0.19	3.74	2.35	0.41	7.17	1.34	1.30
Cameroun & Rio Muni, Guinea Ecuatorial																		
Mean - males	14	48.48	18.71	11.13	3.50	5.33	10.17	3.67	42.01	2.594	1.712	0.188	2.799	1.855	0.348	5.150	0.966	1.155
Standard Error		1.081	0.455	0.531	0.072	0.112	0.333	0.145	0.935	0.0177	0.0600	0.0037	0.0998	0.0504	0.0120	0.1477	0.0301	0.0118
Minimum		42.0	16.3	8.9	3.0	4.8	7.8	3.0	34.7	2.50	1.29	0.16	2.17	1.48	0.26	4.19	0.67	1.07
Maximum		55.2	21.8	15.8	4.0	6.0	12.4	5.2	46.3	2.75	1.98	0.21	3.35	2.10	0.42	5.82	1.13	1.26
Bufo camerunensis Côte d'Ivoire, Ghana, Guinée, Liberia																		
Mean - females	8	71.16	28.79	16.46	4.19	7.63	17.46	4.76	54.71	2.476	1.792	0.146	3.756	1.656	0.241	6.240	0.917	1.289
Minimum		61.9	25.0	13.2	3.1	6.9	15.1	3.3	50.2	2.34	1.39	0.12	2.84	1.47	0.20	4.55	0.67	1.17
Maximum		83.1	34.4	22.8	4.9	9.8	20.0	6.0	66.3	2.60	2.14	0.17	4.76	1.89	0.30	8.64	1.36	1.48

	n	Snout-urostyle	Head width	Head length	Tympanum diameter	Eye diameter	Paratoid length	Paratoid width	Urostyle-heel	SU/HW	HW/HL	T/HW	PL/PW	HW/PL	T/PL	HW/PW	T/PW	SU/UH
Bufo camerunensis Ghana, Liberia, Sierra Leone																		
Mean - males	4	56.15	21.45	13.73	3.73	6.20	13.05	4.40	43.68	2.625	1.567	0.173	2.946	1.705	0.295	4.955	0.858	1.28
Minimum		53.0	19.7	12.7	3.3	5.4	9.7	3.4	40.4	2.37	1.49	0.17	2.52	1.35	0.24	4.48	0.75	1.21
Maximum		61.3	23.5	15.8	4.1	7.0	17.4	4.9	46.9	2.79	1.65	0.18	3.55	2.12	0.36	6.06	1.03	1.35
Bufo camerunensis République Démocratique du Congo																		
female	1	69.5	30.3	17.7	5.6	7.4	16.8	5.9	55.6	2.29	1.71	0.18	2.85	1.80	0.33	5.14	0.95	1.25
Bufo camerunensis République Démocratique du Congo																		
Mean - males	6	53.20	21.28	14.68	4.27	6.13	11.35	4.50	46.43	2.503	1.463	0.200	2.582	1.947	0.387	5.016	0.995	1.147
Minimum		45.4	18.2	10.9	3.2	5.1	6.7	2.5	39.0	2.39	1.34	0.18	1.90	1.64	0.29	3.62	0.72	1.11
Maximum		55.7	23.3	17.0	5.0	6.8	13.9	5.8	50.0	2.60	1.67	0.23	3.28	2.72	0.48	7.28	1.28	1.18
Bufo latifrons Cameroun & Rio Muni, Guinea Ecuatorial																		
Mean - females	4	69.08	24.63	15.98	2.85	7.20	10.80	3.93	58.60	2.808	1.545	0.115	2.930	2.304	0.265	6.596	0.762	1.181
Minimum		66.2	22.8	15.1	2.5	6.8	9.3	2.8	54.3	2.75	1.46	0.11	1.72	2.01	0.24	4.54	0.50	1.12
Maximum		71.3	25.9	17.7	3.2	7.5	12.6	5.4	63.8	2.90	1.62	0.12	3.60	2.63	0.29	8.14	0.89	1.22
Bufo latifrons Cameroun																		
Mean - males	23	49.42	18.84	11.77	2.12	5.93	8.04	3.19	42.37	2.629	1.613	0.113	2.683	2.367	0.265	6.213	0.709	1.168
Standard Error		0.850	0.326	0.271	0.072	0.148	0.193	0.147	0.736	0.0366	0.0349	0.0036	0.1901	0.0612	0.0081	0.3403	0.0539	0.0122
Minimum		39.7	15.3	9.3	1.5	4.4	6.5	1.4	34.2	2.05	1.31	0.08	1.86	1.99	0.19	4.09	0.43	0.98
Maximum		55.7	21.1	14.0	2.8	7.1	10.5	4.4	47.5	2.90	1.98	0.14	6.00	3.08	0.32	12.00	1.57	1.25
Bufo togoensis Togo																		
Mean - females	4.0	68.33	27.18	15.25	3.50	7.90	18.85	5.28	54.63	2.515	1.785	0.129	3.728	1.452	0.188	5.486	0.720	1.251
Minimum		61.8	24.7	14.4	3.1	6.7	17.2	4.2	53.1	2.38	1.65	0.11	2.81	1.28	0.14	3.60	0.40	1.15
Maximum		71.9	28.7	16.7	3.9	8.9	21.6	7.7	56.1	2.61	1.90	0.14	4.33	1.67	0.23	6.83	0.93	1.34
Mean - males	8.0	51.58	19.49	12.36	2.53	6.36	11.94	3.68	43.86	2.647	1.579	0.130	3.365	1.648	0.215	5.488	0.715	1.179
Minimum		47.3	18.1	11.4	2.3	5.3	9.7	2.6	39.1	2.58	1.44	0.12	2.47	1.47	0.17	4.21	0.52	1.10
Maximum		56.3	21.5	13.2	2.8	7.6	13.7	4.8	46.9	2.73	1.73	0.14	4.73	2.04	0.29	7.62	1.08	1.33

	n	Snout-urostyle	Head width	Head length	Tympanum diameter	Eye diameter	Paratoid length	Paratoid width	Urostyle-heel	SU/HW	HW/HL	T/HW	PL/PW	HW/PL	T/PL	HW/PW	T/PW	SU/UH
Bufo maculatus																		
Monrovia, Liberia																		
Mean - females	10	60.62	21.86	12.71	3.95	6.21	12.58	6.52	47.21	2.776	1.743	0.181	2.247	1.759	0.315	3.917	0.709	1.285
Standard Error		1.112	0.455	0.563	0.150	0.115	0.504	1.167	0.703	0.0316	0.0654	0.0061	0.2158	0.0704	0.0079	0.3713	0.0714	0.0213
Minimum		55.8	19.9	10.3	3.2	5.6	10.0	4.0	44.5	2.56	1.46	0.15	0.76	1.54	0.28	1.34	0.23	1.20
Maximum		67.2	24.0	15.8	4.6	6.8	15.1	16.3	50.8	2.93	1.95	0.21	2.91	2.16	0.36	5.40	0.96	1.42
Mean - males	10	52.53	19.30	10.36	3.09	5.90	10.36	4.59	40.64	2.725	1.865	0.160	2.290	1.904	0.308	4.275	0.683	1.293
Standard Error		1.282	0.526	0.287	0.131	0.155	0.589	0.238	0.828	0.0316	0.0305	0.0049	0.1463	0.0993	0.0237	0.1918	0.0341	0.0232
Minimum		45.4	16.1	8.9	2.4	5.3	8.0	3.9	37.0	2.52	1.73	0.14	1.84	1.54	0.22	3.37	0.48	1.23
Maximum		58.0	21.2	12.0	3.7	6.7	13.8	6.3	43.8	2.86	2.01	0.18	3.26	2.59	0.46	5.31	0.86	1.46
Bufo superciliaris																		
Cameroun & République Démocratique du Congo																		
Mean - females	10	128.23	51.07	24.69	5.61	12.72	38.77	13.20	100.69	2.511	2.087	0.110	2.982	1.329	0.146	3.970	0.438	1.283
Standard Error		3.133	0.891	0.921	0.214	0.275	1.255	0.636	3.561	0.0423	0.0658	0.0037	0.1266	0.0473	0.0065	0.2427	0.0330	0.0404
Minimum		117.4	47.6	21.1	4.7	11.0	32.3	9.3	86.0	2.30	1.76	0.09	2.39	1.16	0.12	3.21	0.31	1.07
Maximum		147.0	56.1	30.8	6.7	13.6	46.1	15.4	125.9	2.72	2.42	0.12	3.47	1.56	0.18	5.37	0.63	1.47
République Démocratique du Congo																		
Mean - males	10	114.25	46.12	22.29	5.51	10.67	33.06	11.72	88.08	2.492	2.085	0.121	2.829	1.404	0.168	3.950	0.475	1.297
Standard Error		1.801	1.380	0.815	0.204	0.553	0.960	0.362	1.149	0.0647	0.0752	0.0067	0.0725	0.0514	0.0075	0.1094	0.0248	0.0132
Minimum		108.0	41.7	19.3	4.7	8.4	26.7	10.4	83.7	1.98	1.77	0.09	2.50	1.19	0.14	3.35	0.38	1.25
Maximum		127.5	56.8	26.5	6.6	13.3	38.0	14.0	94.6	2.72	2.55	0.15	3.17	1.69	0.22	4.58	0.63	1.37
Bufo regularis																		
Ogbomosho, Nigeria																		
Mean - females	30	89.91	35.46	20.65	6.89	9.63	24.75	8.05	69.18	2.536	1.718	0.193	3.088	1.442	0.278	4.437	0.861	1.301
Standard Error		2.451	0.955	0.503	0.351	0.193	1.035	0.281	1.848	0.0221	0.0257	0.0082	0.1256	0.0290	0.0087	0.1545	0.0475	0.0184
Minimum		74.6	29.4	18.2	5.1	8.2	19.3	7.0	58.0	2.41	1.62	0.17	2.50	1.31	0.24	3.72	0.68	1.21
Maximum		98.0	38.1	22.6	8.4	10.7	28.8	9.6	75.1	2.62	1.87	0.23	3.65	1.58	0.33	5.25	1.17	1.41
Mean - males	30	81.13	31.87	19.44	5.91	9.23	21.54	6.48	61.58	2.550	1.640	0.185	3.371	1.486	0.276	4.988	0.926	1.321
Standard Error		1.186	0.640	0.345	0.166	0.120	0.635	0.296	1.474	0.0327	0.0240	0.0031	0.1469	0.0310	0.0078	0.1919	0.0429	0.0230
Minimum		76.7	28.8	17.8	5.0	8.8	19.1	5.3	54.5	2.43	1.51	0.16	2.50	1.34	0.23	3.96	0.73	1.18
Maximum		88.2	35.5	21.5	6.8	9.8	24.8	8.0	70.6	2.74	1.74	0.20	4.03	1.64	0.30	5.81	1.13	1.41

	n	Snout-urostyle	Head width	Head length	Tympanum diameter	Eye diameter	Paratoid length	Paratoid width	Urostyle-heel	SU/HW	HW/HL	T/HW	PL/PW	HW/PL	T/PL	HW/PW	T/PW	SU/UH
Bufo xeros N'djamena, Chad																		
Mean - females	5	69.03	24.13	14.2	4.43	7.37	15.25	5.85	47.67	2.861	1.710	0.184	2.625	1.583	0.291	4.153	0.762	1.452
Minimum		67.6	23.4	12.9	4.3	6.9	14.8	5.1	43.0	2.8	1.54	0.18	2.34	1.53	0.27	3.77	0.67	1.33
Maximum		73.6	24.6	15.7	4.6	7.6	15.8	6.4	52.0	3.03	1.85	0.20	3.02	1.62	0.31	4.82	0.88	1.57
Mean - males	10	71	25.37	15.14	4.32	7.5	16.58	6.23	50.41	2.801	1.692	0.170	2.675	1.544	0.263	4.121	0.702	1.413
Standard Error		1.409	0.570	0.566	0.118	0.303	0.681	0.290	1.371	0.0252	0.0577	0.0040	0.0745	0.0472	0.0103	0.1361	0.0261	0.0278
Minimum		60.5	21.9	12.0	3.5	5.6	13.5	5.2	42.5	2.69	1.39	0.15	2.21	1.31	0.21	3.38	0.55	1.27
Maximum		75.9	27.2	17.1	4.8	8.8	20.1	7.8	56.8	2.99	2.10	0.19	3.08	1.87	0.31	4.87	0.81	1.53
Bufo pentoni Senegal																		
Mean - females	10	55.42	20.28	9.44	3.57	6.07	11.8	5.55	40.67	2.735	2.164	0.176	2.159	1.728	0.303	3.719	0.655	1.368
Standard Error		0.907	0.361	0.300	0.118	0.099	0.339	0.231	1.228	0.0328	0.0649	0.0054	0.1030	0.0466	0.0080	0.1850	0.0375	0.0217
Minimum		50.0	18.4	8.1	3.1	5.5	9.9	4.7	34.1	2.59	1.87	0.15	1.41	1.48	0.27	2.71	0.47	1.25
Maximum		59.4	21.6	10.8	4.2	6.6	13.2	7.0	47.4	2.91	2.45	0.21	2.54	1.92	0.34	4.51	0.81	1.51
Mean - males	10	53.31	19.78	9.39	3.58	6	11.33	4.29	39.54	2.696	2.113	0.181	2.657	1.758	0.318	4.625	0.837	1.353
Standard Error		0.982	0.337	0.192	0.121	0.158	0.308	0.103	0.989	0.0313	0.0485	0.0068	0.1026	0.0576	0.0142	0.0946	0.0307	0.0301
Minimum		47.8	17.8	8.5	2.7	5.1	9.9	4.0	33.6	2.50	1.88	0.14	2.06	1.52	0.23	4.04	0.66	1.23
Maximum		60.1	21.7	10.4	4.1	6.8	12.9	4.9	45.4	2.85	2.35	0.21	3.15	1.98	0.40	4.98	1.00	1.57

TABLE 2. Apparent diagnostic differences between linear morphological characters of adult females of *Bufo amieti* and species of *Bufo* from west and central Africa and those all species of the *B. regularis* Comples. * species known from west of the Dahomey Gap. These comparisons are tentative because of the small sample size for *B. amieti* (n=2). A difference (+) indicates that ranges of variation do not overlap. These comparisons cannot be tested for statistical significance because of the small sample size for *B. amieti* and a few of the other species. For data on other species, see Table 7 in Largen *et al.* (1978), Table 12 in Tandy *et al.* (1982) and Tables 1, 9 and 16 in Tandy & Feener (1985).

Species Sex Females	SU	HW	HL	T	E	PL	PW	UH	SU/HW	HW/HL	T/HW	PL/PW	HW/PL	T/PL	HW/PW	T/PW	SU/UH	Diagnostic	Not diagnostic
B. tuberosus	+	+	+	+	+			+						+	+		+	8	9
B. gracilipes				+			+				+			+	+	+	+	7	10
B. villiersi	+	+	+	+	+	+		+		+		+			+	+	+	12	5
*B. regularis**	+	+	+	+	+			+			+	+		+	+	+		11	6
B. superciliaris	+	+	+	+	+	+	+	+	+		+		+	+	+	+	+	14	3
B. garmani	+	+	+	+	+	+		+			+	+		+		+		11	6
B. latifrons	+	+	+	+	+			+					+	+	+	+	+	11	6
*B. togoensis**	+	+	+	+	+	+		+		+		+			+	+	+	12	5
B. brauni	+	+	+	+	+	+		+		+	+	+		+	+	+	+	14	3
B. gutturalis	+	+	+	+	+			+			+	+		+	+	+		11	6
B. kisoloensis	+	+	+	+	+	+	+	+		+	+	+				+		12	5
B. poweri	+	+	+	+	+	+	+	+		+	+	+		+	+	+		14	3
B. rangeri	+	+	+	+	+	+		+				+				+	+	10	7
*B. camerunensis**	+	+	+	+	+	+		+			+	+		+	+	+	+	13	4
B. kerinyagae	+	+			+	+		+				+		+				7	10
*B. xeros**	+	+	+	+	+	+		+			+	+		+	+	+		12	5
B. asmarae	+	+	+	+	+	+		+		+	+	+			+	+		12	5
*B. maculatus**	+	+	+	+	+	+		+			+	+	+	+	+	+		13	4
*B. danielae**	+	+		+	+	+		+			+	+			+			9	8
B. blanfordi			+		+			+							+	+		5	12
B. langanoensis											+	+		+	+	+	+	6	11
B. turkanae	+	+	+	+	+		+	+				+	+	+	+	+	+	13	4
B. perreti	+	+	+	+	+	+		+		+		+	+		+	+	+	13	4
B. steindachneri				+					+		+	+	+	+	+	+		8	9
*B. pentoni**																			
- Senegal	+	+		+	+	+		+		+	+			+		+		10	7

sharp; horizontal diameter of eye greater than length of snout; tympanum distinct, vertically oval, its horizontal diameter 43% that of the eye, 12% that of head width, tympanum diameter (T) 1.8mm, eye diameter (E) 4.1mm; parotoid glands enormous in relation to body size, globose, 1.6 times longer than wide, (PL/PW 1.60), narrowly separated from the eye, the anterior edges lying between the anterior and posterior borders of the tympanum, parotoid length (PL) 9.6mm, 26% of snout-urostyle length, parotoid width (PW) 6.0mm, 63% of parotoid length.

First finger longer than second, second longer than fourth; fingers lacking marginal folds; subarticular tubercles large, undivided; palm with numerous tubercles lacking spinules; inner metacarpal tubercle moderately developed but much smaller than outer metacarpal tubercle and lacking spinules; lacking any series of distinct warts on the posterior surface of the forearm; toes moderately webbed; toe IV with almost four phalanges free of webbing on both the inner and outer margins; most toes

TABLE 3. Variation of nonlinear morphological characters in species of *Bufo* from west and central Africa. * species known from west of the Dahomey Gap. RF - red color on femoral skin. RF - red color on femoral skin. DP - distinct parotoid glands. TF - tarsal fold. WS - white spots on dorsal or lateral skin. VM - ventral mottling. For data on other species, see Table 7 in Largen et al. (1978) and Table 12 in Tandy *et al.* (1982). (1) very few speciments have red femoral color, (2) red on femur in females only; (3) tarsal fold sometimes broken into warts.

Species	n males	females	Total	Sexual dimorphism in gular color color	Vocal sac openings in male: absent	right	left	bilateral	RF	DP	TF	WS present	absent	VM +	(+)	-
*Bufo amieti** - Côte d'Ivoire	0	2	2	?	?	?	?	?	-	+	-	1	1	2	0	0
Bufo tuberosus - Cameroun, Guinea Ecuatorial, République Démocratique du Congo	8	30	38	absent	2	1	3	2	- (1)	+	-	7	31	36	0	2
Bufo gracilipes	10	10	20	present	0	1	1	8	-	weak	-	1	19	17	3	0
Bufo villiersi	6	4	10	absent	0	0	0	5	-	weak?	-	0	8	0	0	8
*Bufo danielae** - Monogaga, Côte d'Ivoire	22	3	25	present	0	11	7	4	-	weak	+	14	11	25	0	0
*Bufo camerunensis** - Cameroun, Côte d'Ivoire, Ghana, Rio Muni-Ecuatorial, Guinée, Liberia, Nigeria, République du Congo, Sierra Leone	17	18	35	present	0	0	0	17	+ (2)	+	+ (3)	1	34	17	8	9
Bufo latifrons - Cameroun & Rio Muni, Guinea Ecuatorial	22	4	26	present	0	0	0	22	+	+	+	1	21	15	6	1
*Buro togoensis** - Togo	6	3	9	present	0	0	0	6	+	+	+ (3)	1	4	4	1	4
*Bufo maculatus**	41	33	74	present	0	18	20	3	+	weak	+	16	57	31	30	15
*Bufo superciliaris** - Cameroun & République Démocratique du Congo	10	10	20	absent	10	0	0	0	+	+	+	8	12	18	0	2
*Bufo regularis**	127	55	182	present	0	0	1	126	- (1)	+	+	85	97	78	0	104
*Bufo xeros**	20	12	32	present	0	0	1	19	+	+	+	1	31	0	1	31
*Bufo pentoni** - Senegal	10	10	20	absent	0	5	4	1	-	weak	+	0	20	0	0	20

with only a slight margin of webbing at the base; webbing with small melanized spinules on the dorsal surface; tubercles of soles smaller than those of palms; inner and outer metatarsal tubercles prominent and suited for burrowing, the inner larger and more raised than the outer. No tarsal fold. Urostyle-heel length (UH) 26.5mm. Dorsum with numerous conical and rounded warts, each with one or more large spinules and some smaller spinules; spinules extending over entire dorsum, including surfaces of parotoid glands, but less numerous anterior to eyes. Venter with somewhat smaller warts with spinules similar to those of the dorsum. Warts at rictus partially fused and covered with numerous small spinules.

Ovaries with immature eggs. The specimen was apparently collected outside of the breeding season.

Color (in alcohol) disruptively patterned light and dark brown; Dorsal background color light brown; four pairs of bilateral reticulate dark brown markings. No *B. regularis*-like white spots on dorsum; No vertebral line; Parotoids and rictal warts same color as dorsum; Dark melanized spinules prominent against lighter background. Lower margin of orbit and part of area beneath eye cream. Upper surfaces of limbs with well defined brown cross bars sometimes outlined in darker brown; posterior femoral integument light brown. Venter markedly reticulately mottled brown and cream. See Figs. 1 - 2.

Paratype: The paratype female is similar to the holotype (Table 1). It is slightly smaller- SU 35.9mm, but is gravid and thus indicates that the breeding season includes December near the beginning of the long dry season. Coloration is like the holotype except overall a somewhat darker brown, and it has a few *B. regularis*-like white spots on the dorsum. See Figs. 3-4.

Geographic distribution and ecology

B. amieti is known from only two localities in lowland rainforest of western Côte-d'Ivoire (Fig. 5). Statistics on the altitude, rainfall and temperature of these localities are given in the diagnosis and in Table 4.

The small number of known localities for *B. amieti* precludes statistical comparisons of ecological variables with other species. Data in Table 4 and 5 indicate some differences and similarities. *B. amieti* seems to differ in one or more ecological characteristics from eighteen of the 25 species with which it has been compared (Table 5), and it is unlikely to be sympatric with any of those. Of the remaining seven species, four, *B. regularis*, *B. superciliaris*, *B. camerunensis* and *B. maculatus*, are known from west Africa west of the Dahomey Gap, but *B. amieti* has not yet been found syntopic with any other bufonid species. *Bufo cristiglans* Inger & Menzies, 1961, is considered a synonym of *B. camerunensis* Parker, 1936.

If *B. amieti* is restricted to relatively undisturbed lowland rainforest, it is unlikely to occur in the same local areas as *B. regularis* or *B. maculatus*. But such a preference for high forest would make it more likely to occur with *B. superciliaris* or *B. camerunensis*. If *B. amieti* does occur locally with these species, it would probably avoid them because the small size of *B. amieti* would make it likely food fare for the other two species.

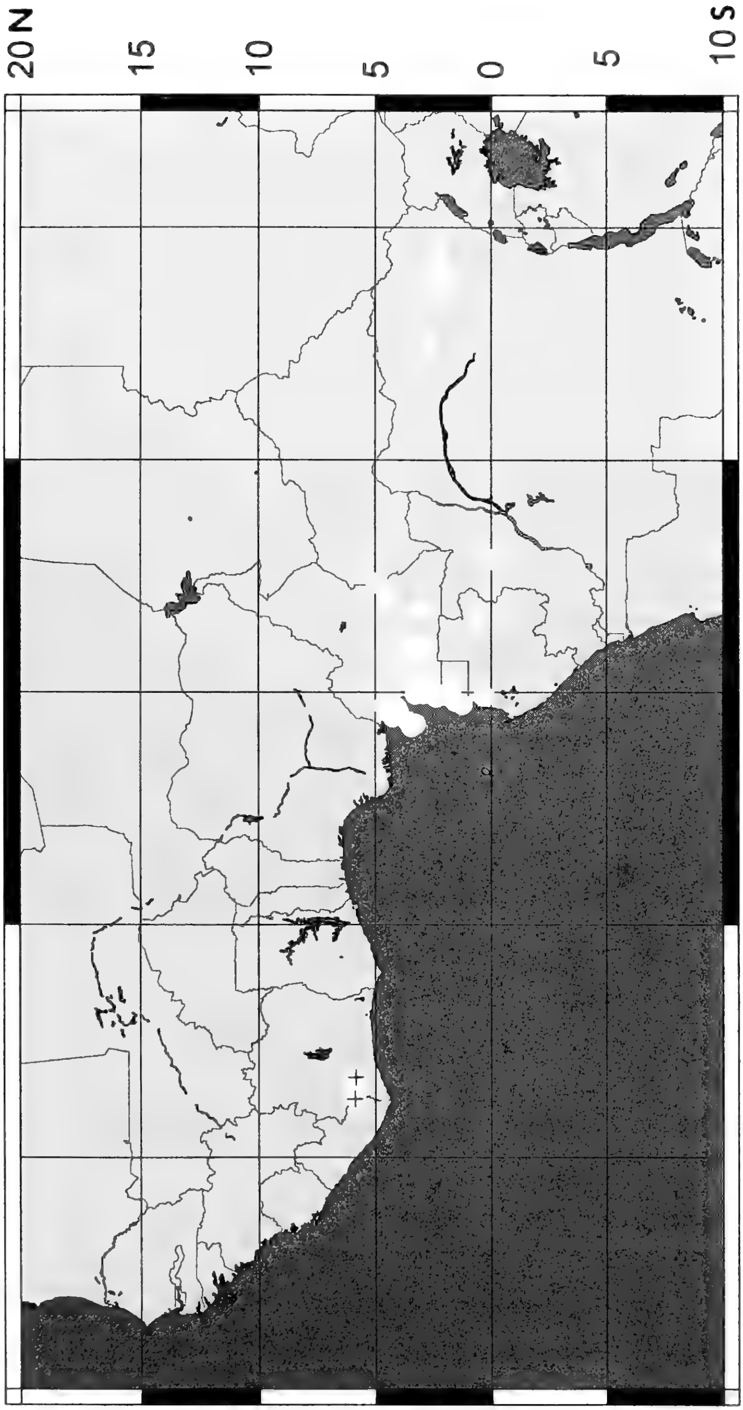

FIG. 5. Known geographic distribution of *Bufo amieti* and *B. tuberosus*. Circles with cross = *B. amieti* sp. n. open circles = *B. tuberosus*.

TABLE 4. Ecological characteristics of *Bufo amieti* and other species of *Bufo* that are known to occur in west or central Africa. Accuracies and sources of these data vary. Some figures are based on surveys or meteorological stations near the locality. Others were interpolated from map contours, isotherms or isohyets. One decimal point given does not necessarily imply such accuracy of measurement but rather that these were the figures used to compute the statistics. Individual values for some altitudes may be in error by 50m or more. Most basic data are from Bartholomew (1985), Knoch & Schulze (1956), NIMA (1999), Wernstedt (1959, 1972) or Survey of Kenya (1962).

	n	Elevation meters	Mean Annual Temp oC	Mean Annual Rainfall cm
Bufo amieti				
Côte d'Ivoire				
Grabazouo		150	23.9	161.1
Taï		123	24	186.3
Mean	2	136.5	23.95	173.7
Bufo tuberosus				
Cameroun, Gabon, Guinea Ecuatorial, République Centrafricaine, République du Congo, République Démocratique du Congo				
Mean		412.8	23.69	224.87
Standard Error		46.63	0.316	20.472
Minimum		10	22	150
Maximum		1266	26.4	411.8
n		48	14	15
Bufo danielae				
Côte d'Ivoire				
Monogaga	1	10	25	150
Bufo camerunensis				
Cameroun, Gabon, Nigeria, République du Congo & République Démocratique du Congo				
Mean	10	526.9	23.1	184.4
Standard Error		95.49	0.49	13.92
Minimum		100	20	140
Maximum		1066.8	24.7	290
Bufo togoensis				
Togo	3	447,3	22.8	141
Minimum		350	22.8	139.7
Maximum		589.8	22.8	142.3
n		3	1	2
Bufo latifrons				
Cameroun & Guinea Ecuatorial				
Mean	5	549.7	24.1	250.9
Minimum		50	22.4	145.3
Maximum		876.9	25.2	350
Bufo maculatus				
Angola, Bissao, Cameroun, Ethiopia, Kenya, Liberia, Mozambique, République Centrafricaine, South Africa, Zimbabwe				
Mean	10	480.5	23.1	163.4
Standard Error		206.62	1.09	44.4
Minimum		19.5	26.7	491.2
Bufo superciliaris				
Cameroun, Ghana, République Démocratique du Congo				
Mean	10	561.1	22.9	193.9
Standard Error		113.59	0.55	13.12
Minimum		50	20	150
Maximum		1066.8	26	260

	n	Elevation meters	Mean Annual Temp oC	Mean Annual Rainfall cm
Bufo regularis				
Algeria, Angola, Cameroun, Egypt, Ethiopia, Gabon, Kenya, Libya, Nigeria, République Centrafricaine, République Démocratique du Congo, Senegal, Sudan, Uganda				
Mean	67	793.6	21.77	102.67
Standard Error		81.16	0.453	8.373
Minimum		7	14	0.3
Maximum		2500	29.6	280
Bufo xeros				
Chad, Ethiopia, Kenya, Uganda				
Mean	10	802.6	23.4	57.8
Standard Error		164.72	1.41	7.8
Minimum		54.9	16	29.9
Maximum		1676.4	29.2	100
Bufo pentoni				
Haute Volta, Senegal, Sudan				
Mean	4	131.5	27.7	40.8
Minimum		5	25	14.9
Maximum		450	29	70
Bufo gracilipes				
Cameroun, Gabon, Guinea Ecuatorial, République du Congo				
Mean	10	310.81	25.52	214
Standard Error		97.57163	0.345704	19.95348
Minimum		10	23	166.4
Maximum		780	27	350
Bufo villiersi				
Cameroun				
Mean	7	1853.5	23.38	263.62
Minimum		1398	22.0	187.7
Maximum		2500	25.0	305.0

B. xeros and *B. pentoni* occur in much drier habitats in the northern portion of West Africa.

B. danielae is known from only two coastal sites in Côte-d'Ivoire (Perret, 1977) which are at lower elevation and appear to have somewhat warmer and drier climates than do the known localities of *B. amieti*.

B. togoensis is known from only three localities that are at higher elevations with somewhat cooler temperatures and lower rainfall than the known sites for *B. amieti*. Tandy (1972) considered *B. togoensis* to be a synonym of *B. latifrons*. Additional recent collections indicate that *B. togoensis* is a distinct species resembling *B. latifrons* in the size and proportions of its tympani and

B. camerunensis in the structure of its parotoid glands.

The ecological features of *B. tuberosus* localities in central Africa do not appear to differ from *B. amieti* sites.

The similarities of both morphology and ecology indicate a close relationship between *B. amieti* and *B. tuberosus*. Apparently *B. amieti* is a western isolate derived from a common ancestor of the two species. This pattern is similar to that of several pairs of lowland rainforest hyperoliid treefrog species east and west of the V-Baoulé

TABLE 5. Apparent differences and similarities between the ecological characteristics of *Bufo amieti* and species of *Bufo* from west or central Africa and those of all species of the *B. regularis* Complex. * species known from west of the Dahomey Gap. These comparisons are tentative because of the small number of known localities for *B. amieti* (n=2). A difference (+) indicates that ranges of variation do not overlap. These comparisons cannot be tested for statistical significance because of the small sample size for *B. amieti* and a few of the other species. (1) - species for which number of localities is less than 10. For data on other species, see Tables 3 in Tandy *et al.* (1976) and Tandy *et al.* (1982), Table 8 in Tandy *et al.* (1985), and Table 13 in Tandy & Feener (1985).

Species compared	Elevation	Mean Annual Temperature	Mean Annual Rainfall	Different	Similar
B. tuberosus	-	-	-	0	3
B. gracilipes	-	-	-	0	3
B. villiersi (1)	+	-	+	2	1
*B. regularis**	-	-	-	0	3
*B. superciliaris**	-	-	-	0	3
B. garmani	-	-	+	1	2
B. latifrons (1)	-	-	-	0	3
B. togoensis(1)*	+	+	+	3	0
B. brauni (1)	+	+	+	3	0
B. gutturalis	-	-	+	1	2
B. kisoloensis	+	+	-	2	1
B. poweri	+	+	+	3	0
B. rangeri	-	+	-	1	2
*B. camerunensis**	-	-	-	0	3
B. kerinyagae	+	+	-	2	1
*B. xeros**	-	-	+	1	2
B. asmarae	+	-	+	2	1
*B. maculatus**	-	-	-	0	3
B. danielae (1)*	+	+	+	3	0
B. blanfordi	+	-	+	2	1
B. langanoensis (1)	+	+	+	3	0
B. turkanae (1)	+	+	+	3	0
B. perreti (1)	+	+	-	2	1
B. steindachneri	-	-	+	1	2
*B. pentoni** - Senegal (1)	-	+	+	2	1

ecological break of Côte-d'Ivoire as described by Schiøtz (1967) for *Hyperolius sylvaticus ivoiriensis* vs *H. s. sylvaticus*, *Leptopelis macrotis* vs *L. rufus* (erroneously as "*L. palmatus*" (Perret, 1973)) and *Leptopelis occidentalis* vs *L. boulengeri*. The initial evolutionary barrier to eastern and western isolates probably is related to changes in Africa's climate during geologic time and particularly to interpluvial periods when the rainforest blocks were probably most isolated.

Bufo tuberosus Günther, 1858

Bufo tuberosus Günther, 1858: 60, pl. 3. fig. C, 140. Peters, 1875: 202. Boulenger, 1880: 546-547, 564, 572-573; 1882: 304. Rochebrune, 1884: 20, 47-49, Pl. IV, Fig. 2. Boulenger, 1887: 565. Bocage, 1895: 15, 272. Werner, 1898: 202. Mocquard, 1903: 215. Boulenger, 1900: 435; 1903: 62. Bocage, 1903: 45. Boulenger, 1906: 158. Johnston, 1908: 950. Nieden, 1908: 509-510, 517. Muller, 1910: 625. Nieden, 1910: 66, 68, Fig 147. Barbour, 1911: 135. Lampe, 1911: 220. Arldt, 1917: 123. Noble, 1922: 39. Nieden, 1923:104. Noble, 1924: 167, 177-178, 311. De Witte, 1930: 241-242, 252; 1934: 167. Loveridge, 1936: 84. Parker, 1936: 155. Mertens, 1938:10; 1941: 277. Monard, 1951: 174. Curry Lindahl, 1956: 56. Perret & Mertens, 1957: 555, 557. Guibé & Lamotte, 1958: 243. Inger & Menzies, 1961: 594.

Mertens, 1965: 14.19. Oates, 1965:89. Perret, 1966: 309-311, 314-315. Amiet & Perret, 1969: 120. Perret, 1971: 131. Perret & Amiet, 1971: 48, 50, 52-53. Amiet, 1973: 136; 1975: 46, 50, 54, 56 (photo); 1976: 150-152 (sonagram); 1978:199. Frost, 1985:63. Amiet, 1989: 92, 95, 98-99 (Pl. I - photo). Brauer, 1991:6, 159, 179.

Bufo polycerus Werner, 1897: 211. Nieden, 1923: 105.

CAMEROUN - Akak-Yemefek; 2°37'N 10°04'E, alt. 50m; ♀ MHNG917.67; 15.V.1955; J.-L. Perret. Batouri; 4°35'N 14°24'E, alt. 655m; ♂ BM1934.12.1.14; IV.1933; M. Merfield. Bibundi (Bibunde); 4°13'N 8°59'E, alt. 50m; (Lampe, 1911). Bipindi; 3°06'N 10°30'E, alt. 200m; 1 specimen; Zenker. (Nieden, 1910). Campo; 2°22'N 9°48'E, alt. 10m; ♀ MHNCF148; I.1947; A. Monard. Ebonji; 4°06'N 9°24'E, alt. 50m; "cri de rivalité" sonagram; (Amiet, 1989, p. 151). Efangono (=?"Efayong"); 3°04'N 11°49'E, alt. 750m; ♀BM1909.7.9.14; 1908?; G. L. Bates. Efulen, Kribi; 2°47'N 10°32'E, alt. 500m; ♂ CNHM3585; Date? ; G. L. Bates. ♀ BM1904. 10.26.28; 1903? ; G. L. Bates. ♀MHNB2482; 1906; Rosenberg. Ekekam III; 3°53'N 11°22'E, alt. 750m; ♂ MHNG1176.5; 10.X.1968. 1 specimen; VI.1968. 3 specimens; X.1968-I.1969. J. -L. Amiet. Foulassi; 2°59'N 11°58'E, alt. 650m; 2 ♂♂ MHNG1008.30-31; ♀MHNG917.66; IV.1953; 4♀♀ MHNG1008.27-29, 1020.47; 8 im. MHNG1008.31-37, 1020.48-49; 1960-61; J. -L. Perret. Gadji; 4°29'N 14°03'E, alt. 600m; ♀BM1937.1.1.21; 1936?; M. Merfield. Idenao; 4°16'N 8°56'E, alt. 100m; 2♀♀ BM1968.470, -.508; 12.VIII.1967; T. Struhsaker. Iemonkonn; 3°54'N 11°58'E, alt. 700m; 1 specimen; I-II/1968. J.-L. Amiet. Kala; 3(51'N 11(22'E, alt. 350m; recording of mating call; 12.I.1972; 2 specimens; VII-X.1967; 2 specimens; 15.II-15.IV.1969. J. -L. Amiet. Kendonge (Kidonge), S. Bakundu Forest Reserve; 4°33'N 9°26'E, alt. 50m; ♂ BM1969.1635; ♀ BM1969.509; 1968?; S. Gartlan. Kribi (includes "Dja River" of MCZ record); 2°56'N 9°56'E, alt. 43m; ♀ MCZ2660; 1908; G. H. Schwab. 3♀♀UMMZ 35611; I-VI.1907; 38320; 1908; 56277; no date; G. H. Schwab. Kumba (=Johann-Albrechtshöhe); 4°38'N 9°25'E, alt. 200m; 2 specimens; Conradt. Nieden, 1910). Limbe (Victoria); 4°01'N 9°12'E, alt. 100m; 4 specimens ZMB?13915; Preuss. (Nieden, 1908, 1910). 32 km N Lolodorf; 3°26'N 10°42'E, alt. 250m; ♂ CAS103353 (TP3545); 21-22.III.1966; T. Papenfuss. Lomié District; 3°09'N 13°35'E, alt. 632m; ♀ BM1937.12.1.54; 1936?; M. Merfield. Mabiogo; 2°12'N 9°53'E, alt. 10m; ♀ MHNCF88; 28.II.1947; A. Monard. Mbanlam; 3°17'N 9°54'E, alt. 612m; ♂ MHNG955.100; 27.IX.1957; J. -L. Perret. Momobelenga; 3°56'N 11°40'E, alt. 600m; ♂ sonagram of mating call; Date?; (Amiet, 1976, p.151). Mundame; 4°35'N, 9°31'E, alt. 100m; 2 specimens; 1906; Rohde. (Müller, 1910). Ngam/Sangmelima; 2°47'N, 11°54'E, alt. 759m; 3 ♀♀ MHNG955.97-99; 4.I.1957, 3.III.1957, 20.IX.1957; 1 specimen SMF52335; 17.VI. 1955; J. -L. Perret. Nkolfep; 3°59'N 11°24'E, alt. 350m; 1 specimen; II.1968; J. -L. Amiet. Nta Ali; 5°33'N 9°30'E, alt. 1266m; ♂; 15.IV.1977; J. -L. Amiet (Amiet, 1978). Rio del Rey; 4°44'N 8°37'E, alt. 50m; 1886?; H. H. Johnston. (Bouleng-er, 1887). Sangmelima (includes "Zima Country" of BM records); 2°56'N 11°59'E, alt. 782m; 2♀♀ BM1906.5.28.150-151; 1905?; G. L. Bates. ♂ CNHM19918; 1899; A. I. Good. nr Ting (32 km S Akonolinga) Sta. 141; 3°40'N 12°10'E, alt. 750m; record-ing of mating call, ♂ MT.TC.CA123; 7.IV.1971. M. & J. Tandy. Yapoma (nr Douala); 4°02'N 9°49'E, alt. 50m; ♀ZMB27541; 1910; Schafer. No locality; ♂ ZMB8319; 1870-1880; A. Reichnow.
GABON - Makokou; 0°34'N 12°52'E, alt. 516m; ♂ MHNG2207.33 (MBG1117); 25.X.1964; ♀ MHNG2207.34 (MBG1277); 26.XI.1964; L. P. Knoepffler. Nzing-Ayong (=?Nzibelong); 0°18'N, 9°50'E, alt. 50m; 2♂♂ MHNG2207.31-32 (MBG129, 336); ♀MHNG2207.30 (MBG128); 26.III.1964; L. P. Knoepffler.
GUINEA ECUATORIAL - *Bioko (Fernando Poo)*: Basilé (Bassilé), slopes of Pico de Basilé (Santa Isabel); 3°36'N 8°45'E, alt. 527m; 2 adults MB; 1894?; F. Newton. (Bocage, 1895, 1903-1905). Rio Iladyi Falls, south of Bioko (Moca); 3°20'N 8°40'E, alt. 914m; ♀BM1969.2447; 18.IX.1964; University College Expedition. Luba (Bahia de San Carlos); 3°27'N 8°33'E, alt. 400m; im. SMF?; 20.IX-24.X.1962; R. Mertens. (Mertens, 1965). Moca (Moka); 3°20'N 8°40'E, alt. 914m; ZMB333999; XI.1939; H. Eidmann. (Mertens, 1941). Musola; 3°26'N 8°37'E, alt. 500-800m; (Boulenger, 1905-06). San Antonio de Ureca; 3°16'N 8°39'E, alt. 10m; ♀ZFMK9291; I.1963; M. Eisentraut. No specific locality; ♀BM1947.2.21.14(=BM1851-10.25.7) Holotype; 1850; Fraser?

Rio Muni: Cabo San Juan (Cape St. John); 1°15'N 9°30'E, alt. 50m; Martinez de la Escalera. (Boulenger, 1903). Macomo (Makomo); 1°43'N 9°49'E, alt. 350m. (Nieden, 1908). Rio Uoro-Rio Mbini (Rio Benito); 1°34'N 9°38'E, alt. 50m; 4 ♀♀ BM1900.2.17.109-112; 1899; G. L. Bates. Rio Lana 2.4km N Evinayong; 1°39'N 10°39'E, alt. 750m; ♀BM1965.1412; 6.IX.1965; J. Oates. No locality; ZMB20035; Date?; Collector?
République du Congo *(Congo-Brazzaville)* - Djamba; 0°05'S 15°43'E, alt. 350m; RG3159; XII.1924; H. Schouteden. (De Witte, 1930).
République Démocratique du Congo *(Belgian Congo; Zaire)* - Bafwabaka; 2°10'N 27°50'E, alt. 750m; ♀AMNH8405; 1909-1915; Congo Expedition. Buta; 2°47'N 24°47'E, alt. 350m; 2 specimens RG4402-03; II.1925; G. F. De Witte. Epulu; 2°15'N 29°15'E, alt. 350m; 2 specimens; 9.IV.1952. K. Curry-Lindahl. (Curry-Lindahl, 1956). Kifuku (s/la Nawa); , alt. ; RG1595; VIII.1925; H. Schouteden. Medje; 2°25'N 27°18'E, alt. 750m; RG1054; IV-V.1910; Lang & Chapin. Medje; 2°25'N 27°30'E, alt. 750m; AMNH8404; IV-V.1910; Congo Expedition. (Noble, 1924). Ngayu; 1°40'N 27°40'E, alt. 750m; AMNH8401-02; IV-V.1910; Congo Expedi-tion. (Noble, 1924). (Note: AMNH8403 is a ♂ *Bufo funereus*.)
République Centrafricaine - Tibili (=?"Tuburi, Narob"); 4°58'N 14°42'E, alt. 750m; ♀BM 1912.1.11.19; 1911?; P. A. Talbot.

Morphology

Many aspects of the morphology of *B. tuberosus* have been described and illustrated in the literature. Illustrations include drawings in Günther (1858), Rochebrune (1884) and Nieden (1910) and photographs of preserved material in Perret & Amiet (1971) and of living specimens in Perret (1966) and Amiet (1975, 1989).

Plate 1. *Bufo tuberosus* female, Ngam, Sangmelima, Cameroun.

TABLE 6. Some diagnostic differences between linear morphological characters of adults of *Bufo tuberosus* and species of *Bufo* from west and central Africa and those all species of the *B. regularis* Complex. * species known from west of the Dahomey Gap. A difference (+) indicates that ranges of variation do not overlap. Lack of a diagnostic difference does not indicate lack of a statistical difference. These comparisons have not been tested for statistical significance. For data on other species, see Table 7 in Largen *et al.* (1978), Table 12 in Tandy *et al.* (1982) and Tables 1, 9 and 16 in Tandy & Feener (1985).

Species Sex Females	SU	HW	HL	T	E	PL	PW	UH	SU/HW	HW/HL	T/HW	PL/PW	HW/PL	T/PL	HW/PW	T/PW	SU/UH	Diagnostic	Not diagnostic
*B. amieti**	+	+	+	+	+			+						+		+		8	9
B. gracilipes	+	+	+			+	+	+										6	11
B. villiersi																		0	17
*B. regularis**																+		1	17
*B. superciliaris**	+	+	+	+	+	+		+				+		+				9	8
B. gammani												+				+		2	15
B. latifrons															+	+		2	17
*B. togoensis**						+						+						2	15
B. brauni	+	+		+	+	+						+				+		8	9
B. gutturalis												+			+	+		3	14
B. kisoloensis				+														1	16
B. poweri	+	+		+		+						+				+		6	11
B. rangeri	+	+						+				+				+		5	12
*B. camerunensis**																+		1	16
B. kerinyagae						+						+	+			+		4	13
*B. xeros**	+	+		+		+		+				+				+		7	10
B. asmarae	+					+		+				+	+			+		6	11
*B. maculatus**																+		1	16
*B. danielae**	+	+						+				+						4	13
B. blanfordi	+	+																2	15
B. langanoensis												+				+		3	14
B. turkanae	+	+						+				+			+	+		6	11
B. perreti									+			+			+	+		4	13
B. steindachneri	+	+	+				+	+				+				+		7	10
*B. pentoni** - Senegal			+													+		2	15
Males																			
*B. amieti**	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
B. gracilipes		+						+										2	15
B. villiersi	+	+				+		+										5	12
*B. regularis**												+				+		2	15
*B. superciliaris**	+	+	+	+	+	+	+	+	+			+	+			+		12	5
B. garmani	+	+	+	+	+	+		+				+				+		9	8
B. latifrons																+		1	16
*B. togoensis**												+				+		2	15
B. brauni	+	+	+	+	+	+		+				+				+		9	8
B. gutturalis	+	+	+	+	+	+						+	+		+	+		10	7
B. kisoloensis	+	+	+			+						+				+		6	11
B. poweri	+	+	+	+	+	+	+	+		+		+				+		11	6
B. rangeri	+	+	+	+	+	+		+				+	+			+		10	7
*B. camerunensis**												+				+		2	15
B. kerinyagae	+					+						+				+		5	12
*B. xeros**	+	+		+		+		+				+				+		7	10
B. asmarae	+					+		+				+				+		5	12
*B. naculatus**																+		1	16
*B. danielae**																+		1	16
B. blanfordi							+											1	16
B. langanoensis												+				+		3	14
B. turkanae												+			+	+		3	14
B. perreti												+				+		2	15
B. setindachneri												+				+		3	14
*B. pentoni** - Senegal												+				+		2	15

Günther's description focused on the extreme wartiness of the skin, but did not give measurements or ratios of body parts. The sex of the holotype was not specified nor was its exact locality on the island of Bioko (Fernando Poo) (Günther, 1858). Boulenger later published a more detailed description with some measurements and verbal proportions, however he mistakenly identifed the holotype as a male and his measurements for that specimen differ from ones made more recently.

The very prominent parotoids were noted by Boulenger (1880) and by subsequent authors such as Noble (1924), Perret (1966) and Perret & Amiet (1971). The data in Tables 1 and 6 demonstrate the markedly low ratio of parotoid length to width and also the very small size of the tympanum compared to parotoid width. The ratio of T/PW separates *B. tuberosus* diagnostically (ranges of variation do not overlap) from 18 (in females) or 21 (in males) of the 25 other African *Bufo* species compared. As summarized in Table 6, *B. tuberosus* differs diagnostically in at least one of these measurements or their ratios from all of the species compared except for females of *B. villiersi.*

Boulenger (1900) mentioned a crimson vertebral line in some specimens from the Rio Uoro (Rio Benito), Rio Muni, Guinea Ecuatorial. That color has now faded in those specimens.

Noble (1924) noted variation in ventral coloration in his material from the eastern République Démocratique du Congo ranging from heavy to no dark mottling.

Parker (1936b) gave ratios of body to foot length and interpreted this as demonstrating relatively short legs of *B. tuberosus* compared to other species. Perret (1966) gave ranges of variation of body and tibia lengths for each sex and ratios of parotoid gland length/width and body length/tibia length. These data do not appear to support Parker's appraisal of relative leg length, although Perret did not give arithmetic means of his ratios (only ranges) nor did he test such for statistical significance. Although differences of means given in Table 1 have not been tested for significance, the data on ratios of snout-urostyle length/urostyle heel length do not support Parker's judgement about leg length in this species. Those data indicate that *B. tuberosus* is one of the longer legged species.

Perret (1966) noted the marked sexual dimorphism of body size in this species. Tables 1 and 7 illustrate this dimorphism in linear characters. All measurements are at least statistically smaller in males than females, and two are diagnostically different. Most ratios do not differ between the sexes, although females have statistically narrower heads relative to body size (SU/HW) and smaller tympani relative to parotoid width (T/PW).

TABLE 7. Sexual dimorphism of linear morphological characters in *Bufo tuberosus*. D - difference diagnostic, ranges of variation do not overlap. S - statistically significant difference $P < 0.01$. - no statistical difference

																Number of characters		
SU	HW	HL	T	E	PL	PW	UH	SU/HW	HW/HL	T/HW	PL/PW	HW/PL	T/PL	HW/PW	T/PW	SU/UH	Diagnostic	Statistical	Not diagnostic
D	S	S	S	S	S	S	D	S	-	-	-	-	-	-	S	-	2	8	7

Perret (1966) stated that he had not found vocal sac openings in males except for one with a single opening on the left. Perret & Amiet (1971) made a similar statement. Table 3 shows numbers and locations of vocal sac openings in the eight adult males examined. Two lack openings.

MATING CALL

Basic physical structure. The mating call of *Bufo tuberosus* is a series of low pitched hooting sounds that lack the noisy quality of the calls of most African *Bufo*. They are also not as loud as those of many other species (Amiet, 1976). The physical structure of these calls is similar to that of species of the *B. regularis*, *B. maculatus*, *B. blanfordi*, *B. funereus* (except *B. villiersi*), and *B. pentoni* groups and also some species of the *B. vertebralis* Complex and *B. angusticeps* group (Tandy, 1972; Tandy & Keith, 1972; Tandy & Tandy, 1976). Each complex pulse train (series of hoots) contains a variable number of simple pulse trains repeated at a rate of about 1.6 per second in specimens from Cameroun (Table 8). Each simple pulse train contains about 17 passive pulses repeated at a rate of 87 per second (89.74/sec at about 24°C). The duration of simple pulse trains is about 0.2 second (.18 at 24°C). The low emphasized frequency is the dominant frequency at about 526Hz. Sonagrams show three harmonics above the low emphasized frequency, but these contain less than half the energy of the low emphasized frequency. These frequencies show a slight gradual rise at the ends of simple pulse trains. These data are based on calls of only two recorded specimens. See material studied for times and places.

Amiet (1976) described and illustrated a sonagram of a call of a male *B. tuberosus* uttered while trying to clasp a plastic bag containing another male which Amiet termed a "cri de rivalité". This call is structurally very similar to male release calls uttered by many Bufo species, and the context indicates that is what it was. It is very different from the mating call in structure and function.

TABLE 8. Physical characteristics of the mating calls of *Bufo tuberosus*. PPR = passive pulse repetition rate; NPP/PT = number of passive pulses per simple pulse train; PT DUR = simple pulse train duration; PTR = simple pulse train repetition rate; LOW EMP = low emphasized frequency; DOM = dominant frequency; n = number of individuals per sample.

	N	PPR (/sec)	NPP/PT	PT DUR (/sec)	PTR (/sec)	LOW EMP (Hz)	DOM (Hz)
Bufo tuberosus							
Kala, Cameroun	1	84.80	18.60	0.230	1.30	547.0	547.0
Sta. 141 nr Ting, Cameroun	1	89.74	15.96	0.178	1.92	505.0	505.0

Circadian and seasonal calling behavior. In April, 1971, Tandy found a mixed chorus of *Bufo gracilipes* and *B. tuberosus* calling along a small stream at dusk in secondary forest near Ting, Cameroun. The *B. gracilipes* called in water holding onto living aquatic plants and vegetative debris in the middle of the stream. *B. tuberosus* called from very well-concealed sites among overhanging roots of forest vegetation beneath the undercut stream bank. Amiet (1973, 1976, 1989) was able to make

additional observations of this behavior. The above two species and *B. villiersi* are the only Camerounian *Bufo* known to typically call during daylight, and these species are atypical of most species in the genus.

Amiet (1976) has found that *B. tuberosus* choruses are usually small, often less than a dozen individuals. He also observed one larger aggregation near YaoundÈ, Cameroun.

In Cameroun, *B. tuberosus* breeds during the dry season and at the beginning of the rainy season ñ principally January-March (Amiet, 1976).

Comparisons with other species. The mating call of *B. tuberosus* is as distinctive as its morphology. Table 10 compares the acoustic structure to those of twenty African species including all species whose mating calls are known from west and central Africa and all members of the *B. regularis* Complex (Tandy & Tandy, 1976). See also data in Tandy *et al.*, 1976; Largen *et al.*, 1978; and Tandy *et al.*, 1982 and 1985. The call of *B. tuberosus* appears to differ diagnostically (ranges of variation do not overlap in data available) in at least 3 characters from all twenty species. This comparison must be considered tentative because of the small sample size (2) available for *B. tuberosus*, but the comparisons are probably valid because of the much larger data sets available for most of the other species.

Only *B. gracilipes* has been observed calling at the same time and locality as *B. tuberosus*, although *B. camerunensis* has been observed breeding nearby. Other species of the central African rain forests that might breed in the same areas include *B. latifrons*, *B. maculatus* and *B. superciliaris*. The latter is thought to lack a mating call (Amiet, 1976).

The call of *B. tuberosus* differs in five of six apparently homologous characters from *B. gracilipes*, *B. villiersi* and *B. perreti* and it also differs qualitatively from those species. The mating calls of the above three species are first order sequences of complex pulse trains whereas that of *B. tuberosus* is just one complex pulse train.

The voice of *B. camerunensis* differs in all six call characters compared. The PPR is slower in *B. camerunensis*, the NPP/PT and PT DUR two to three times greater and PTR is one third to one fourth its rate in *B. tuberosus*.

The mating call of *B. latifrons* is different in all six characters. PT DUR in *B. tuberosus* is about one fifth, PPR is more than three times faster and PTR is two to four times faster than in *B. latifrons*.

The voice of *B. maculatus* differs in four characteristics. PPR and PT DUR are about twice, NPP/PT four times and PTR up to twice greater than in *B. tuberosus*.

The call of *B. regularis* differs in three characters. PPR is less than a third, PT DUR is about four times greater and PTR less than one half those in *B. tuberosus*. These two species are not likely to be sympatric because of different habitat preferences.

None of the other species in Table 9 is likely to be sympatric with *B. tuberosus*. Their calls differ from the latter species in at least three characters.

TABLE 9. Apparent differences and similarities between the mating calls of *Bufo tuberosus* and 19 species of *Bufo* from west or central Africa and all those known of species of the *B. regularis* Complex. * species known from west of the Dahomey Gap. ^ species of central Africa. These comparisons are tentative because of the small number of specimens recorded for *B. tuberosus* (n=2). A difference (+) indicates that ranges of variation do not overlap. These comparisons cannot be tested for statistical significance because of the small sample size for *B. tuberosus* and a few of the other species. (1) - species for which number of specimens analyzed is less than 10. For data on other species, see Table 1 in Tandy *et al.* (1976), Table 2 in Largen *et al.* (1978), Table 1 in Tandy *et al.* (1982), and Table 14 in Tandy & Feener (1985). (2) Comparison is between homologous characters rather than those of the same grade of physical compexity (See Tandy & Tandy, 1976).

Species compared	PPR	NPP/PT	PT DUR	PTR	LOW EMP	DOM	Number of characters Different	Similar
*B. gracilipes^*	+	+ (2)	+ (2)	– ?	+	+	5	1 ?
B. villiersi ^(1)	+	+ (2)	+ (2)	– ?	+	+	5	1 ?
B. regularis^*	+	–	+	+	–	–	3	3
B. garmani	–	+	+	–	–	+	3	3
B. latifrons ^(1)	+	+	+	+	+	+	6	0
B. brauni	-	+	+	+	+	+	5	1
B. gutturalis	+	-	+	+	-	-	3	3
B. kisoloensis ^(1)	-	+	+	+	-	+	4	2
B. poweri	+	+	+	-	-	+	4	2
B. rangeri	+	+	-	-	+	+	4	2
B. camerunensis^*	+ ?	+	+	+	+	+	6	0
B. kerinyagae (1)	+	+	+	+	+	+	6	0
B. xeros^*	+	+	-	-	+ ?	+ ?	4	2
B. asmarae	+	+	+	+	-	+	5	1
B. maculatus^*	+	+	- ?	- ?	+	+	4	2
B. langanoensis (1)	+	+	+	+	+	+	6	0
B. turkanae (1)	+	-	+	+	+	+	5	1
B. perreti	-	+ (2)	+ (2)	+ ?	+	+	5	1
B. steindachneri^(1)	+	+	-	-	+	+	4	2
B. pentoni^* - Senegal *(1)*	+	+	+	+	+	+	6	0

GEOGRAPHIC DISTRIBUTION AND ECOLOGY

Bufo tuberosus is known from fiftyone equatorial lowland rainforest localities in Cameroun, Guinea Ecuatorial (Bioko and Rio Muni), Gabon, République du Congo, République Centrafricaine and République Démocratique du Congo between latitudes 0°5'S and 5°14'N and longitudes 8°33' and 29°15'E (Fig. 5). These are in an altitudinal range of 10 to 1266m. See Table 4 for climatic data.

Ecological data in Tables 4 and 10 indicate that *B. tuberosus* localities differ diagnostically from those of fifteen of the 25 species compared. *B. tuberosus* is not likely to be sympatric with any of those.

Among the remaining ten species, seven occur in central Africa, *B. gracilipes*, *B. superciliaris*, *B. latifrons*, *B. camerunensis*, *B. maculatus* and *B. steindachneri*. As noted above, *B. tuberosus* has been found syntopic only with *B. gracilipes*. But it is likely to occur within close proximity of all of these except *B. steindachneri*. The latter occurs primarily in marshy sites surrounded by arid savanna.

B. tuberosus is known only from forested localities, so it is not so likely to occur with *B. regularis* or *B. maculatus* which often prefer more open habitats.

The other high forest species, *B. gracilipes*, *B. superciliaris*, *B. latifrons* and *B. camerunensis* are most likely to occur with *B. tuberosus*.

As noted previously, the ecology of *B. tuberosus* sites is very much like that of the allopatric *B. amieti*.

TABLE 10. Apparent differences and similarities between the ecological characteristics of *Bufo tuberosus* and species of *Bufo* from west or central Africa and those of all species of the *B. regularis* Complex. * species known from west of the Dahomey Gap. ^ species known from central Africa. Some of these comparisons are tentative because of the small number of known localities for some species. A difference (+) indicates that ranges of variation do not overlap. These comparisons have not been tested for statistical significance. (1) - species for which number of localities is less than 10. For data on other species, see Tables 3 in Tandy *et al.* (1976) and Tandy *et al.* (1982), Table 8 in Tandy *et al.* (1985), and Table 13 in Tandy & Teener (1985).

Species compared	Elevation	Mean Annual Temperature	Mean Annual Rainfall	Different	Similar
B- Amieti (1)	-	-	-	0	3
B. gracilipes ^	-	-	-	0	3
B. villiersi ^ *(1)*	+	-	-	1	2
B. regularis *^	-	-	-	0	3
B. superciliaris *^	-	-	-	0	3
B. garmani	-	-	+	1	2
B. latifrons ^ *(1)*	-	-	-	0	3
B. togoensis (1)	-	-	+	1	2
B. brauni (1)	-	+	-	1	2
B. gutturalis	-	-	+	1	2
B. kisoloensis ^	-	+	-	2	1
B. poweri	-	-	+	1	2
B. rangeri	-	+	-	1	2
B. camerunensis *^	-	-	-	0	3
B. kerinyagae	+	+	-	2	1
B. xeros *^	-	-	+	1	2
B. asmarae	-	-	+	1	2
B. maculatus *^	-	-	-	0	3
B. danielae * *(1)*	-	-	-	0	3
B. blanfordi	-	-	+	1	2
B. langanoensis (1)	-	-	+	1	2
B. turkanae (1)	-	+	+	2	1
B. perreti (1)	-	-	-	0	3
B. steindachneri^	-	-	-	0	3
B. pentoni *^ - Senegal (1)	-	-	+	1	2

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